The growth response of selected Zambian hardwood species to changing climatic conditions

by

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Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch University will not infringe any third-party rights and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

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Abstract

Factors such as precipitation and temperature are key to the growth of trees. The expected change in growing conditions, i.e. rise in temperature and reduction in precipitation will influence tree growth, wood structure and on wood quality. Due to lack of instrumental data, little is known about how Miombo trees growing in Zambian Miombo woodlands have responded to climate change. The objective of this study was to examine the extent to which climate variables related to water availability and temperature during cambial periods shape wood anatomical properties of three hardwood species growing in Miombo woodlands in Zambia, namely *Brachystegia spiciformis, Burkea africana,* and *Isoberlinia angolensis*. The species were selected based on value, distribution across the climate zones, dendrochronological potential, and relative ease of coring. To understand how Miombo trees growing in Zambia have responded to climate change, the ring structure and wood anatomical properties were related to known extreme climatic events. Sample materials, in the form of increment cores, were collected from areas differing in water availability. From the three climate zones, sites with climate data were selected and their aridity determined based on mean annual precipitation and mean annual temperature using De Martonne's Index. At each site, 15-20 living trees were selected for sampling. For each tree, diameter at breast height (1.3 m), total height, bole height, and crown diameter were measured, after which two increment cores were then obtained from breast height at 90° and 180° to the wind direction. After collection, the cores were labelled to indicate site name, species, tree number, and core number for ease of identification in the lab and then placed in a core holder. In the lab, the cores were prepared for ring measurement and analysis using standard dendrochronological procedures after drying. The cores were then placed on a wooden mount and their ring structure studied under a microscope attached to a computer with ring measurement and analysis software. For wood anatomical studies, a Nano-CT scanner was used to obtain images from prepared cross sections representing wood formed during dry and very wet years.

To compare the growth response of each species to different sites, ring structure was studied. Ring analysis revealed that mean sensitivity negatively correlated very well with mean annual precipitation. For all the species, sensitivity was significantly different between dry and wet sites. Sensitivity was high on the drier sites while complacent growth occurred on the wetter sites. In all the species, about 20% of the ring width variance could be explained by precipitation, but growth was unresponsive to temperature.

The second part of the study looked at how the trees responded to extreme climate events. Each of the species was looked at separately. In all the species, data analysis revealed statistically significant ($p<0.05$) differences in fibre and vessel characteristics between those formed during wet and dry

years, and those from dry and wet sites. Studies on effect of ring width on density revealed that, typical of diffuse-porous woods, density was independent of ring width.

Fit functions developed from models based on projected values of precipitation under climate change scenario RCP8.5 revealed that cell wall thickness, which will increase by an average of +10.6 µm in all the species, will have the biggest influence on wood density. Wood quality will therefore change because of climate change.

The study proved that in the absence of long-term data measured across the climate zones on the same trees, tree-ring studies can provide answers to questions on how particular trees react to adverse effects of climate change.

Opsomming

Faktore soos reënval en temperatuur is die sleutel tot die groei van bome. Die verwagte verandering in groeitoestande, as gevolg van klimaatsverandering, d.w.s. styging in temperatuur en vermindering in reënval, sal boomgroei, houtstruktuur en houtkwaliteit beïnvloed. Dit is onseker hoe Miombo-bome wat in die Zambiese Miombo-woude groei, sal reageer op hierdie klimaatsverandering. Die doel van hierdie studie was om te ondersoek in watter mate die klimaatsveranderlikes die houtanatomiese eienskappe van drie loofhoutsoorte wat in Miombo-boslande in Zambië groei, naamlik *Brachystegia spiciformis, Burkea africana* en *Isoberlinia angolensis*, beïnvloed. Die spesies is gekies op grond van waarde, verspreiding oor die klimaatsones, dendrochronologiese potensiaal en relatiewe gemak van inkrement-boring. Steekproefmateriaal, in die vorm van inkrementboorsels is versamel van gebiede wat verskil in die beskikbaarheid van water. Van die drie klimaatsones is terreine met klimaatdata gekies en hulle droogheid is bepaal op grond van gemiddelde jaarlikse reënval en gemiddelde jaarlikse temperatuur met behulp van De Martonne se Indeks. Van elke terrein is 15-20 bome gekies vir steekproefneming.

Ringstruktuur is bestudeer om die groeireaksie van elke spesie op verskillende terreine te vergelyk. Ringanalise het getoon dat gemiddelde sensitiwiteit negatief korreleer met gemiddelde jaarlikse neerslag. Vir al die spesies was sensitiwiteit aansienlik verskillend tussen droë en nat plekke. Sensitiwiteit was hoog op die droër terreine, terwyl selfbewuste groei op die natter terreine plaasgevind het. Vir al die spesies kon ongeveer 20% van die ringwydte-variasie verklaar word deur reënval - en groei het nie op temperatuur reageer nie. Tipies vir diffeus-poreuse hout, was digtheid onafhanklik van ringwydte.

In die tweede deel van die studie is die reaksie op uiterste klimaatgebeure geanaliseer. Vir elke spesie en terrein is een uiters nat en droë jaar gekies vir houtanatomiese studies. Vir alle spesies was verskille in vesel- en seleienskappe tussen dié wat gedurende nat en droë jare gevorm is, en dié van droë en nat plekke, statisties beduidend.

Fit funksies ontwikkel uit modelle gebaseer op geprojekteerde waardes van neerslag onder klimaatsverandering scenario RCP8.5 het getoon dat die selwand dikte, wat met 'n gemiddeld van +10.6 µm in al die spesies sal styg, met die grootste invloed op houtdigtheid het. Houtkwaliteit sal dus verander as gevolg van klimaatsverandering.

Dedication

This thesis is dedicated to the enduring memory of Mr. Joseph H.J. Mweene. For dedicating this piece of academic work to a man who is not among us, I humbly seek the indulgence of the many living friends and close relatives. I have a simple reason for doing so: without him, the potential in me may never have been realised.

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I owe my family a debt of gratitude for putting up with my lengthy absences.

Dear God, thank you.

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List of Acronyms and Abbreviations

AAO	Antarctic Oscillation
AEZ	Agro-ecological zones
CAB	Congo air boundary
CT	Computed Tomography
CWT	Cell wall thickness
DBH	Diameter at Breast Height
DJF	December, January, February
DMI	De Martonne's Index of aridity
ENSO	El Niño Southern Oscillation
FAO	Food and Agriculture Organisation
FD	Fibre diameter
GRZ	Government of the Republic of Zambia
IOD	Indian Ocean dipole
IPCC	Intergovernmental Panel on Climate Change
ITCZ	Inter-Tropical Convergence Zone
MAP	Mean Annual Precipitation
MAT	Mean Annual Temperature
ppm	parts per million
RW	Ring width
SAWS	South African Weather Service
SST	Sea surface temperature
TSAP	Time Series Analysis and Presentation
UNFCCC	The United Nations Framework Convention on Climate Change
USAID	The United States Agency for International Development
VD	Vessel diameter
WMO	World Meteorological Organisation

Chapter 1 General Introduction

1.1 Introduction

In the last century, there have been significant changes in the three main factors that determine plant growth: precipitation, temperature and atmospheric CO_2 concentration (Hegerl *et al.* 2007). Available data shows that global average temperature has risen by 0.6±0.2°C, while mean surface temperature across Africa increased by 0.5-2°C (Houghton *et al.* 2001) and this observed temperature increase exceeds that attributed to natural climate variability (IPCC 2007a). Climate change's impact will differ by country and region, and will depend on prevailing conditions (FAO 2012). Projections by the Intergovernmental Panel on Climate Change (IPCC) are that Africa will suffer great and early damage as a result of climate change (IPCC 2007a), with the impact being more severe in areas where water availability already limits tree growth (Claesson and Nycander 2013). Southern Africa, which according to the Köppen climate classification system is broadly divided into dry and moist mild-latitude climates (Lohmann *et al.* 1993), experiences considerable annual and inter-annual rainfall and temperature variability (Sithole and Murewi 2009) due to its geographic position and differences in the major climatic influences and topographic features (Reason *et al.* 2006; Davis 2011; WMO 2014). Evidence shows that significant changes in certain climate variables have taken place in the region. Minimum, average and maximum temperatures across much of Africa show an upward trend (Chidumayo *et al.* 2011), which is projected to be higher than the global mean (IPCC 2007a). Davis (2011) reported a 0.27°C rise in annual minimum temperature, while annual maximum temperature rose by 0.25°C after 1976, which was found to be statistically significant at a 95% confidence interval. Davis further reported that, post 1995, the highest observed maximum temperature began to rise at a statistically significant rate of 0.85°C per year.

Analysis of 1960-2003 climate data for Zambia by McSweeney *et al.* (2008) revealed that mean annual temperature (MAT) had risen by 1.3°C, an increase of an average of 0.29°C/decade. The increase in winter temperature increase, at an average rate of 0.34°C per decade, was higher. McSweeney *et al.* (2008) and World Bank (2018) also reported that "hot" days and "hot" nights increased by an average of 43 per year while "cold" days and "cold" nights decreased by 22 and 35, respectively. Jury (2013) concluded that the departures from the 1961-1990 mean indicate that Southern Africa is getting constantly warmer.

One of the main factors influencing climate in the region is the El Niño Southern Oscillation (ENSO), which strongly influences rainfall patterns, not just in Zambia, but the entire region and causes large inter-annual variability (World Bank 2018). Though variability is normal, records indicate that significant changes have taken place regarding rainfall in Southern Africa (New *et al.* 2006). Over

the last six decades, mean annual precipitation (MAP) in some parts of Africa has declined by as much as 30%, while droughts have increased (Sivakumar *et al.* 2005). In Zambia, MAP has reduced at a rate of 1.9 mm per month (2.3%) per decade since 1960. The reduction in annual rainfall has been greater (at a rate of 7.1 mm per month) during the December – February period. This is the core of Zambia's rainy season (McSweeney *et al.* 2008). Detection of changes in rainfall for the region is not easy because of differences in place-to-place variability (Vogel 1994; Fauchereau *et al.* 2003; Davis 2011). In the coming decades, Miombo woodlands are likely to see significant changes in growing conditions. For trees growing on water-limited sites, a further increase in temperature coupled with a reduction in rainfall will mean significant decreases in growth.

1.2 Background

Availability and quality of forests and tree resources shape life in Africa (Chidumayo *et al.* 2011). Throughout the world, concern over climate change has increased due to its expected impact on the environment and natural resources (Sango *et al.* 2015; Bonal *et al.* 2016). The expected climate change will have an impact on tree growth through rainfall, temperature and extreme weather events (Buchanan *et al.* 2008). Buchanan *et al.* (2008) further explain that the impact of climate change on forests and trees depends on how the changing climatic variables interact with growth limiting factors, i.e. length of growing season, soil water availability, etc.

Change in climate has implications not only on tree growth but also on wood quality. Climate change may have both beneficial and detrimental effects to tree growth. In cold regions, climate change will probably foster an increase in growth rate, whereas in warm regions, where trees are already subjected to soil water scarcity and heat stress, it may threaten the survival of species and entire forest communities in regions (FAO 2012). Response to CO_2 fertilization will vary by species (Steffen and Canadell 2005) but due to increased photosynthesis (Fairbanks and Scholes 1999; Eamus and Ceulemans 2001) it is expected to be positive (Long and Ainsworth 2004; Ainsworth and Rogers 2007; Kirilenko and Sedjo 2007; Goklany 2015). While photosynthesis will increase due to elevation of CO_2 levels, stomatal conductance will decrease (Wagner *et al.* 2012; Bonal *et al.* 2016) and reduced water availability will counter growth increase (Buchanan *et al.* 2008; Brzostek *et al.* 2014). An increase in temperature in cold regions will lengthen the growth period, resulting in gains in productivity (IPCC 2007b), but higher temperatures may reduce water availability and have a negative impact on forests' net primary productivity (Pittock 2003, 2009).

1.3 Problem statement

Variation in environmental conditions affects tree growth and wood properties, which in turn have implications on its processing and on the quality of the end products. The knowledge base regarding

impact of climate change on African forests and tree resources is weak (Chidumayo *et al.* 2011). In Zambia, not much is known regarding the response of hardwood trees due to the absence of continuous plot data measured on the same trees and species or forest levels across the climate zones.

The aim of this study is to establish how hardwood species growing in the Miombo woodlands found in Zambia have over time and across different climate zones responded to changing climatic conditions. The specific objectives of the study were to:

- Compare the growth response of three different Miombo species to different climatic conditions (i.e. water availability and temperature)
- Determine the effect of climatic conditions on wood growth through the analysis of tree rings and wood anatomical properties
- Attempt to predict how wood quality of the selected species will change with the expected climate change

Based on their distribution across the climate zones, their ease of coring, dendrochronological potential, and value attached to them, three Miombo species (*Brachystegia spiciformis, Burkea africana,* and *Isoberlinia angolensis)* were sampled. These are dominant canopy species, especially in the high rainfall areas. The average air-dry densities of the species are: 780 kg/m^3 (*Brachystegia spiciformis*)*, 820* kg/m^3 (*Burkea africana*) and 820 kg/m^3 (*Isoberlinia angolensis*) (Dyer *et al.* 2016). Wood from these tree species has been used for construction, mine props and as railway sleepers. It is also suitable for flooring, veneer and plywood, door frames, furniture and joinery, pulpwood and as an energy source in smelting copper, production of charcoal and simply as firewood (Oyen and Louppe 1912; Maroyi 2010; Oyen 2012).

Significant variation in growing conditions due to change in climate could result in lower quality of wood from these and other Miombo tree species. The more variation in properties, the less suitable the wood will be, especially for applications in which strength is the key consideration. Variation in properties will make it difficult for the timber from these species to fulfil explicit or implicit design strength requirements.

1.4 Structure of the dissertation

This dissertation consists of an introduction, a chapter detailing the experimental methods, followed by three chapters discussing tree-ring analysis, analysis of wood anatomical properties and a chapter attempting to use these properties to predict the effect that the expected climate change will have on the wood quality if the studies species.

Appendix A contains signed declarations by the candidate and each co-author regarding the nature and extent of the contributions the different authors made to the papers.

Chapter 2 has been published as a review article: The Expected Effects of Climate Change on Tree Growth and Wood Quality in Southern Africa. Munalula F, Seifert T, Meincken M. (2016) Springer *Science Reviews,* 4, 99-111.

Chapters 4 and 5 have been submitted for publication

Growth response of three Miombo tree species to climatic effects. Munalula F, Seifert T, Meincken M, submitted to Forest Ecosystems.

Assessing the effects of extreme climate events on selected anatomical properties of three Miombo species growing in Zambia. Munalula F, Seifert T, Meincken M, submitted to the IAWA (international association of wood anatomists) Journal.

Chapter 2 The Expected Effects of Climate Change on Tree Growth and Wood Quality in Southern Africa

2.1 Introduction

Climate, defined as the average long-term atmospheric condition of a place (IPCC 2012; WMO 2015), results from the complex interaction of the ocean, atmosphere, geosphere, cryosphere and biosphere (Treut *et al.* 2007; Patakas 2012). On a more local level, these global processes are further modified by the orography, the living environment, and at a plant level by factors, such as temperature, solar radiation, precipitation and vapour pressure deficit. Regarding climate change, the focus often is on long-term changes of average values. However, there is mounting consent that weather extremes should be included in a realistic characterization of climate, in addition to long-term averages (Eagleman 1985; CDST 1988).

2.2 Climate of Southern Africa

The Southern African sub-region is characterized by tropical and subtropical climate (WMO 2015) and has been described as a mostly semi-dry region (Davis 2011a) with significant inter-annual, inter-decadal and multi-decadal climate and rainfall variability (Mason and Jury 1997; Dilley 2000; Reason *et al.* 2006; Christensen *et al.* 2007; Davis 2011). The region, except for the Mediterranean Climate of the Western Cape of South Africa, is mainly characterized by a wet and hot summer season (October to March) and a cool and dry winter (April to September) (SAWS 2015; WMO 2015). Tadross and Johnston (2012) and Jury (2013) report that although the climate systems governing Southern Africa's seasonal weather remained the same for decades, some variations in values of climate elements governed by changes in climate forcings take place from season to season. Several factors determine the differences in climate regimes across the region (Davis 2011).

2.2.1 Major Climate Influences

The major factors determining the Southern African climate are governed by the geographical position of the sub-region (Davis 2011a), with the most influential climate factors being ocean currents, the Inter-Tropical Convergence Zone (ITCZ) and quasi-stationary high-pressure systems (Reason *et al.* 2006; WMO 2015). Mason (2001), McSweeney *et al.* (2008) and Davis (2011) point out that the ITCZ and the Congo air boundary (CAB) affect climate by creating a major zone of convergence and rainfall; anticyclones suppress the ITCZ circulation and a thermal low-pressure system found over Botswana and Namibia, extending at times into Zambia and the Democratic Republic of Congo, breaks up the anticyclone circulation. The E Niño Southern Oscillation (ENSO) additionally changes the position of the ITCZ and creates conditions for enhanced or restricted

rainfall, and tropical cyclones bring excessive precipitation and flooding to coastal regions. Tadross and Johnston (2012) state that in addition to ENSO, the other important drivers of rainfall variability are the Antarctic Oscillation (AAO) and the Indian Ocean dipole (IOD).

However, the most important example of natural climate variability on inter-annual timescales is the ENSO phenomenon which consists of a warm phase (El Niño) and a cold phase (La Niña) and is considered the leading cause of climate variability on a global scale (Reason and Mulenga 1999; Davis 2011a). ENSO is a phenomenon that takes place because of increased sea surface temperatures (SST) in the central Pacific (Mason 2001) and it not only drives inter-annual rainfall variability in Southern Africa (Ropelewski and Halpert 1987; Lindesay 1998; SAWS 2015) but also determines the ons*et al* of the rainy season and the frequency of dry spells within it (Reason *et al.* 2006). El Niño years occur when there is largescale warming of surface water in the central and eastern equatorial Pacific Ocean and there are changes in the tropical atmospheric circulation (i.e. winds, pressure and rainfall) (WMO 2015). During El Niño years, Southern Africa receives less than average rainfall and during La Niña years more than the average for the region (Ropelewski and Halpert 1987; Mason 2001; SAWS 2015), which affects, for example, Zambia substantially. Based on mean annual precipitation (MAP) received, Zambia is divided into three agro-ecological zones: Zone 1 (MAP\800 mm); Zone II (MAP = 800–1000 mm); and Zone III (MAP 1000 mm) (Eroarome 2009). An analysis of various sites across Zambia shows that El Niño years result in drier than average conditions in the normally wet summer months in the dry sites in the southern half of the country, whilst the *wet* sites in the north of the country simultaneously experience significantly wetter-than average conditions (McSweeney *et al.* 2008).

However, the South African Weather Service (SAWS 2015) argues that ENSO explains only about 30% of the rainfall variability. Other factors should, therefore, also be considered when predicting seasonal rainfall. Apart from El Niño, SST also significantly affects the Southern African climate (Reason and Mulenga 1999; Tadross and Johnston 2012; Jury 2013). The increasing SST of the Indian Ocean, an effect observed since the late 1970s, results in drier weather conditions inland. (Reason and Mulenga 1999) found statistically significant increases in rainfall over large areas of eastern South Africa and neighbouring regions because of increases in SST resulting from changes in the convergence of moist air streams originating from the Indian Ocean and from tropical southern Africa. Because of its location and the fact that it is surrounded by two oceans with very different temperatures, Southern Africa is extremely vulnerable to climate variability and climate change (Naidoo *et al.* 2013).

2.2.2 Climate Change in Southern Africa

Climate change, whether caused by human activities (Wigley 1999; UNFCCC 2011; IPCC 2013) or natural variability (IPCC 2001; Davis 2011), describes persistent long-term changes to predominant climatic conditions (Davis 2011; IPCC 2012).

Several studies (such as Kruger and Shongwe 2004; Archer and Tadross 2009; Chidumayo *et al.* 2011; Howarth 2012; Lesolle 2012) have found clear evidence that across large areas of Southern Africa, temperatures are increasing, whereas rainfall is declining. In addition, the region has experienced several climatic hazards and extreme events that represent significant departures from the 1961 to 1990 average state of the climate system (Davis 2011a; Funder *et al.* 2013).

In major parts of Africa, the observed surface temperatures have shown an accelerating warming trend since 1960, reaching +0.03°C/year in places (Conway *et al.* 2004; New *et al.* 2006; New 2015). The Inter-Governmental Panel on Climate Change (IPCC 2014a) states that large parts of Southern Africa have experienced an increase in annual mean, maximum and minimum temperatures and reports that land surface warming in Southern Africa is expected to be higher than the global mean land surface temperature increase in all seasons (IPCC 2007c, 2013), with the drier sub-tropical regions warming more than the moister tropics (Christensen *et al.* 2007; Chidumayo *et al.* 2011). For example, a study of Zambia's climate records for the last four decades has established that mean annual temperature (MAT) has increased by 0.6°C per decade (GRZ 2010), with daily temperature observations showing significant increases in the occurrence of hot days and nights in all seasons (McSweeney *et al.* 2008). Ziervogel *et al.* (2014) report that for South Africa, there has been a $1\frac{1}{2}$ times rise in average temperatures each year compared to the observed global mean of 0.65°C since the 1960s, with extreme precipitation events also increasing in frequency.

The change in precipitation patterns in the tropics and sub-tropics has been much more regional compared to the temperature patterns and variable over a multi-decadal scale (Hulme *et al.* 2001; IPCC 2001). Several authors (Christensen *et al.* 2007; Parry *et al.* 2007; Chidumayo *et al.* 2011; Pettorelli *et al.* 2012) agree that there has been a general decline in rainfall across much of Africa, with IPCC (IPCC 2007c) and Glantz *et al.* (2007) reporting that in large areas of Southern Africa a downward trend in precipitation has been observed since 1950 and that years with below normal rainfall are becoming more and more frequent. Although the long-term trends are weak (Richard *et al.* 2001) and inter-annual variation in rainfall is an expected part of the Southern African climate, variations have increased since 1970 (Usman and Reason 2004). Reason *et al.* (2006) found a strong relationship between ENSO and the start of the rainy season and frequency of dry spells within it. For Zambia, weather data of the last five decades indicate that El Niño episodes are occurring more regularly at lower intervals, resulting in an increase in frequency and magnitude of

floods and droughts (Mason 2001; GRZ 2010; Lesolle 2012), as well as changes in the onset, cessation and duration of the rainy season in the sub-region (Lesolle 2012). In Zambia, for example, droughts occurred in 1991/92, 1994/95 and 1997/98 (Urquhart and Lotz-Sisitka 2014). Between 2000 and 2007, Zambia experienced two drought years, two flood years and two years of rain that can be regarded typical for the country (Urquhart and Lotz-Sisitka 2014).

In conclusion, it is predicted that mean temperatures are likely to increase in Southern Africa, following the global trend. Precipitation will react more locally and erratically, and it will be difficult to anticipate the possible consequences. However, there is mounting evidence that the MAP will decrease, and the frequency of droughts will increase, also triggered by more frequent El Niño occurrences.

In addition, a likely scenario of the expected climate change is that more intense wild fires will occur frequently, because of a rise in temperature and the frequency of dry spells (Odhiambo *et al*. 2014), which could cause additional stress to trees. However, the understanding of the correlation between climate change and fires is still incomplete (Macias-Fauria *et al.* 2011).

With this expected climate change, the major driving forces of tree growth could change, and growth patterns and wood formation can be expected to change accordingly.

2.3 Tree Ring Analysis as a Research Tool to Trace Climatic Influence

Tree rings have been widely used as a tool to trace climate influence on trees. This is possible because tree rings reflect climatic signals. However, tree growth is also controlled by genetics and the interaction of genetic and environmental factors (Kozlowski and Pallardy 1997) and differs in temperate and tropical regions due to differences in environmental conditions. In temperate regions, trees undergo an annual cycle composed of a growth period in spring and summer and a dormant period in autumn and winter (Fritts 1976; Kozlowski 1984; Kozlowski and Pallardy 1997). During each growing season, trees produce a new layer of wood towards the outer part of the tree trunk just inside the bark. The seasonal variation in temperature is the main climatic variable driving this growth pattern (Borchert 1999), resulting in the creation of annual rings. However, tree rings are rarely formed close to the equator due to persistently homogenous growth conditions. Depending on conditions, tree growth may occur all year around and, in such cases annual rings may not be visible (Kozlowski and Pallardy 1997). On the other hand, sub-tropical forests are subjected to high seasonal and inter-annual variation in environmental conditions (Nath *et al.* 2006), which might lead to visible tree rings. The main growth stimulus for tropical trees is not temperature-related but rather water-controlled (Worbes 1999). In tropical countries with a dry season of at least three months, rainfall seasonality constitutes the primary determinant of cambial dormancy and ring formation, and

annual rings are induced by annually occurring dry periods or flooding (Worbes 1995; Trouet *et al.* 2010).

As opposed to primary growth, which occurs in the apical meristems and results in the increase in length of the shoot and the root, secondary growth is the growth that results from cambial activity, which causes the stems and roots to thicken as the plant grows older (Everett *et al.* 2015; Taiz *et al.* 2015). Long-term climate data are a prerequisite for the study of climate effects on secondary growth and development (Bradley *et al.* 1996), but the availability of reliable long-term climate data is limited in most of Africa (Anyamba and Eastman 1996).

In many countries, eco-physiological growth models are used to run scenario simulations on the impact of climate change, which model the impact of growth factors on tree growth directly (Bossel 1991; Keenan *et al.* 2008). These are, however, not available for the indigenous trees of Southern Africa, as eco-physiological growth models require typically species-specific data. Southern Africa has a multitude of species, and most of the data on the influence of growth factors of the various trees are not available (Battaglia and Sands 1997; Rötzer *et al.* 2009; Fontes *et al.* 2010). Due to the high amount of information necessary for the calibration of ecophysiological process models, these have only been developed, calibrated and applied for a few commercial plantation species such as Eucalyptus and Pine in Southern Africa (e.g. Gush 1999; Dye *et al.* 2004).

While an ecophysiological process modelling approach seems currently out of reach for most indigenous forest systems in Southern Africa, the effect of changes on climate on tree growth can be also studied without long-term records of diameter growth and climate information. For this, a retrospective analysis of growth rings and wood anatomy can be applied (Jacoby and D'Arrigo 1997; Downes *et al.* 2002), which partially substitutes long-term longitudinal studies with cross-sectional studies on sites of different climatic conditions, if the relation between tree ring width or certain anatomical properties and climatic conditions holds also for tree rings where no weather data are available. This can be done, because tree rings represent the net product of physiological processes that occur seasonally, which is recorded in the wood structure as rings (Fritts 1976; Downes *et al.* 2009). The sequence of wide and narrow growth rings visible on the cross section of a tree stem is indicative of changes in wood anatomy and might be correlated to variations in growing conditions (Fritts 1976). These growth responses to known climatic conditions can also be used to project how wood growth—and with it the wood properties—could change with different scenarios of climate change in the Southern African region.

Seasonal patterns of wood growth may be typically related to water availability (Worbes 1999) and for this reason dendrochronological methods developed for temperate zones (Schweingruber 1988) can be applied for many tropical areas with a dry season of more than 2 months (Worbes 1992,

1995). Tree ring analysis makes use of the fact that there is large variation of wood properties in radial direction of the stem, especially in regions with seasonal climate (Downes *et al.* 2009). Tree-ring analysis of tropical trees has been carried out for more than one hundred years (Worbes 2002) but its wide application in Southern Africa had been hampered by the belief that tropical trees do not produce annual rings (Worbes 1995). Cook *et al.* (1992) list indistinct tree-ring boundaries, severe wedging of rings, short life spans and inadequacy of possibly useful species as some of the problems encountered in tree ring analysis of tropical trees in the past. However, as stated above, Southern Africa is predominantly sub-tropical and contains warm temperate and Mediterranean areas as well. Studies on several hardwoods from the Miombo woodlands and Afrotemperate forest have shown the presence of distinct ring boundaries and statistically significant links between rainfall and variations in growth (Fanshawe 1956; Geldenhuys 2005; Grundy 2006; Schweingruber 2007; Syampungani *et al.* 2010; Trouet *et al.* 2010; Jooste 2015).

2.4 Tree Reaction to Climatic Change

To understand tree reaction to climate change, knowledge of two generic concepts is helpful: the stress concept and the concept of limiting factors.

2.5 The Stress Concept and Plant Response

Macedo (2012) defines stress as the internal or external negative effect that an organism may suffer. Stress can be caused by biotic agents, such as competing trees or pathogens, or it can be of abiotic origin, which is the focus of this study. Nilsen and Orcutt (1996) defined stress more generally as the condition induced by external factors that result in the alteration of equilibrium, which regards a response that can either be positive or negative. Gaspar *et al.* (2002) point out that not all deviations of growth patterns from the optimum will necessarily cause stress, if the plants are flexible and acclimatised to their environment.

Abiotic stress plays a critical role in determining the geographical distribution of tree species (Harfouche *et al.* 2014). Abiotic stress is determined by interactions between organisms and their physical environment (Ahmad and Prasad 2012; Duque *et al.* 2013). It includes a host of factors, such as salinity, metal toxicity, nutrient deficiency, temperature stress (both extreme heat and extreme cold), water stress (flooding and drought), or fire (Harfouche *et al.* 2014). Abiotic stress can thus be attributed to changes in direct growth factors (nutrients, CO_2, light, water), or factors that inhibit growth and damage the tree (ozone, fire, wind). The dominant environmental factors that determine the size of the layer of wood added each growth season are precipitation, solar radiation (quality and quantity), temperature and relative humidity (Coder and Warnell 1999; Nabeshima *et al.* 2010; Bareja 2011). Körner (2006) states that since plants commonly cannot move, they must cope

with prevailing environmental conditions. Because of this immobility and because trees are long living organisms, they are confronted with varying stress situations in their lives (Rötzer *et al.* 2012), many of which have a detrimental effect on growth and development (Browse and Farmer 2013). Rötzer *et al.* (2012) state that plant stress is typically described by its frequency, intensity, duration and time of occurrence.

Plants react to changes in their environment by means of strategies that are either ecological or evolutionary in nature (Jump and Penuelas 2005; Anderson *et al.* 2012). Any change in climate has many potential effects on plants, some detrimental to growth, others beneficial (Kirschbaum *et al.* 1996). Larcher (2003) cited in Lichtenthaler (998) explained that when plants are exposed to stress, the physiological functions are first destabilized, after which normalization and improved resistance occur. When the plant's tolerance limits are exceeded, permanent plant tissue damage or death of the plant may be the result (Rötzer *et al.* 2012). Trees react to abrupt, periodic environmental changes, which usually have a catastrophic or at least a severely damaging effect on plants, as well as to permanent changes in environmental conditions (Schweingruber 2007b).

2.5.1 The Concept of Limiting Factors

As pointed out before, climatic changes often affect growth factors directly and, in this context, the concept of limiting factors is an important consideration. Tree growth is limited under normal conditions by competition for the main growth resources and by external, environmental factors (Kozlowski and Pallardy 1997; Ahmad and Prasad 2012), such as dehydration stress due to drought and high temperatures (Vorasoot *et al.* 2003; Jaleel *et al.* 2009). The concept of limiting factors follows Liebig's Law of the Minimum, which states that the rate of plant growth, the size to which it grows, and its general health are dependent on the amount of the scarcest essential growth factor (Allaby 2006). Growth is therefore controlled not by the total amount, but by the most limiting resource and no biological process can take place faster than the most limiting factor allows (Fritts 1976; Haferkamp 1988; Nabeshima *et al.* 2010; Hasanuzzaman *et al.* 2013; Yamori *et al.* 2014). This simple concept explains a lot of observations made in plant growth studies.

In a Southern African context, solar radiation becomes limiting only in dense high forest stands, such as the Afromontane forests or commercial forest plantations, where at some growth stages a sensitivity for light competition can be detected (Seifert *et al.* 2014). In woodlands and savannahs, trees are spaced more loosely, so that solar radiation is usually not limiting but rather providing access to water and nutrients (Frost 1996). Water availability has a pivotal role, since it is not only needed as a chemical component for photosynthesis, but it also controls transpiration, as closed stomata inhibit gas exchange of the leaves. Thus, a lack of water will inevitably also lead to a lack of mineral nutrients in the crown (Ferguson 1959; Lambers and Chapin III 1998; Jenks and Hasegawa

2014). Fritts (1976) argued that in studies correlating ring width and drought, the use of trees growing on the driest site is recommended, because these are individuals, in which ring width is the most likely to have been limited by water stress.

2.5.2 Tree Sensitivity to Climatic Changes and Adaptation Patterns

Trees are specifically affected, since they live comparatively long and can take some time until they bear fruit and can regenerate (Downes *et al.* 2002). To survive in the face of climatic changes, trees develop mechanisms of tolerance, resistance or avoidance (Macedo 2012). How a plant responds to changes in environmental conditions depends largely on its resource requirements (Chapin *et al.* 1993). An important factor to consider is that trees incur change in their sensitivity to environmental factors with age (Coder and Warnell 1999; Ward *et al.* 2006; Seifert *et al.* 2014) As they age, they accumulate energy reserves that enable them cope better with changes in environmental conditions and making them less susceptible to stress. Studies on tree response to water related stresses have shown that when soil water availability drops below a certain threshold, trees adapt a variety of drought avoidance strategies, which can be of short-term eco-physiological, longer-term morphological and allometric nature or even genetically developed traits at the species level (De Micco and Aronne 2012a).

2.5.3 Long-Term Coping Strategies of Allocation Pattern and Morphology

Plants respond to stress in a variety of physiological and biochemical ways at cellular and organism levels, which occur over various lengths of time. In the long-term, due to adaptations plants can develop strategies to maintain a high-water potential in conditions where water availability inhibits plant growth (Jenks and Hasegawa 2014). They thus develop tolerance, i.e. the ability to withstand a particular stress condition. Trees can balance the demands of the leaves with the root system's ability to collect moisture and nutrients (Ward *et al.* 2006). As a response mechanism, roots adjust their growth and water transport properties (Patakas 2012). As soil water availability is reduced (Davies, 2006), water uptake by roots is reduced, but control of water loss is mainly due to stomatal control (Taub 2010; Claesson and Nycander 2013).

2.5.4 Seasonal Response Patterns

On a global scale (Rehman *et al.* 2005), water is a major determinant in the distribution of species, and the responses and adaptation of the species to water stress are critical for their success in any environment. Maximov (1931) cited by De Micco and Aronne (2012) reported that trees cope with increased heat and water stress by being dry-season deciduous, thus restricting growth events to times when enough water is available (Grene *et al.* 2011). Dropping leaves during drought saves potential water loss through transpiration (De Micco and Aronne 2012a). Cambial activity resumes

when the growth limiting environmental factors improve. During periods of drought the plant response of dry-deciduous trees can involve stomatal closure, deceleration or complete cessation of growth and premature leaf fall (Körner 2006). In Southern Africa, *Brachystegia spiciformis* is an example of a species that experiences leaf-fall due to short-term drought (Trouet *et al.* 2012).

2.6 Effects of Climatic Factors on Tree Physiology, Growth and Wood Anatomy

Even if it must be acknowledged that frequently limiting growth factors occur simultaneously (Jenks and Hasegawa 2014), it is of value to consider them separately in order to gain a clear understanding of the reactions of trees to certain situations.

2.6.1 Water Availability

As pointed out before, Southern Africa is characterized by a high variability in precipitation. As a consequence, trees may experience limited water availability of variable duration (Jenks and Hasegawa 2014). Plants can be stressed by the lack of water, as well as the excess of water (Haferkamp 1988) which is tolerated by some plants for certain time, but not by all (Kozlowski 1984b). In the dry environment of Southern Africa, drought is the more frequently found stressor. Edmond *et al.* (1979) found that under conditions of high absorption and low transpiration rates, maximum swelling of the cells occurs due to a build-up of turgor pressure in regions where the cells are elongated. Plants typically loose water through transpiration and failure to absorb adequate water to counter loss causes water stress in the plant. This leads to withering, stoppage of growth, or even death (Gindaba 2004) and when water stress is combined with an increase in temperature it imposes fundamental limits to forest productivity (Teskey *et al.* 1987). Though aridity interferes with typical growth, disrupts water relations and negatively affects water-use efficiency (Aroca 2012) plants respond to water stress in a variety of physiological and biochemical ways at cellular and organism levels, which occur over various lengths of time (Farooq *et al.* 2009).

2.6.2 Temperature

During their life, plants are exposed to different day and night temperatures (Kramer and Kozlowski 1960). Maximum plant growth takes place at day temperatures of between 5.5 and 8°C above the night temperature. Within this temperature range, the optimum day temperature facilitates photosynthesis and respiration during the daytime, while the cooler night curtails respiration rate (Murphy and Lugo 1986). A definition of extreme temperature is difficult, because most plants tolerate a wide range of temperatures. For each plant, a set of cardinal temperatures exists that control its growth and existence (Fowells and Means 1990a). These are the minimum and maximum temperature, which limit growth and the temperature, at which maximum growth is reached. The ideal temperature range for survival of plants is 0 to 50°C (Bareja 2011). Fowells and Means (1990)

state that for most tropical plants the minimum is around 10°C, the maximum 50°C and the optimum ranges from 30 to 35°C.

In trees, the key factors which determine the thermal death threshold are the duration of high temperatures, the maximum temperature, the tree age, mass and moisture content and how well the tree species responds to temperature changes (Decoteau 1998; Hasanuzzaman *et al.* 2013; Hatfield and Prueger 2015).

Temperature affects trees directly and indirectly. A direct impact on trees is heat stress, which disturbs the normal cellular homeostasis leading to retardation of growth and development and even to death due to the denaturation of enzymes in extreme conditions (Mathur *et al.* 2014) or cell and tissue damage (De Melo-Abreu *et al.* 2010).

Temperature affects trees indirectly through transpiration. As temperature increases, a vapour pressure deficit can occur, which leads to a closure of stomata, despite sufficient soil moisture being available (Ryan 2010). In this case, the water is not transported fast enough to the leaves, which leads to a stomata closure (Matala *et al.* 2005; Allen *et al.* 2010; Claesson and Nycander 2013).

Photosynthesis is very sensitive to stress caused by high temperatures and is typically inhibited before other cell functions are impaired (Mathur *et al.* 2014). In addition, respiration increases drastically with increasing temperature, roughly doubling with every ten degrees increase in temperature (Turnbull *et al.* 2001) and consequently the rate of net photosynthesis declines rapidly above a critical temperature, which varies with species, because the photosynthates are used faster than they are produce (Weiss and Berry 1987; Turnbull *et al.* 2001; Hemsley *et al.* 2004). Climate change models project a MAT increase of about five degrees Celsius for Southern Africa (Moss *et al.* 2008; Davis 2011b), which roughly equals an increase of respiration of 30–40% (Reich *et al.* 2016). For Zambia, the mean annual temperature is projected to increase by 1.2–3.4°C by the 2060s, and 1.6–5.5°C by the 2090s (McSweeney *et al.* 2008). By regulating the respiration after exposure to higher temperature, plants can acclimatise to slight increases in temperature. While increased temperatures generally accelerate tree growth in cool temperate and boreal regions, it does not have positive effects in the tropics, since tropical trees are mostly already close to their temperature optimum (Way and Oren 2010). Morecroft and Paterson (2006) state that even where precipitation patterns do not change, a rise in temperature will have an impact on the water balance of vegetation through a rise in evapotranspiration. It will likely lead to an increase in the recurrence and severity of aridity conditions, which in turn could negatively affect growth and survival of certain species due to increased risk to the tree's hydraulic system (IPCC 2001; Allen *et al.* 2010).

2.6.3 Carbon dioxide (CO_2)

Records show that the concentration of CO_2 in the atmosphere has steadily increased from about 385 parts per million (ppm) (Ziska and Bunce 2006; Keeling 2009) to more than 400 ppm (Tans and Keeling 2014; Vaughan 2015; Blasing 2016). CO_2 does not only affect the climate, through the greenhouse effect (Claesson and Nycander 2013; IPCC 2013), but also the growth, physiology and chemistry of plants (Cure and Acock 1986; Taub 2010). Because of the effect of ''CO_2 fertilisation'' resulting from increasing CO_2 concentration in the air, plants tend to grow better (Jacoby and D'Arrigo 1997). As CO_2 levels rise, the photosynthesis rates tend to increase. Increased exposure to elevated CO_2 and temperature are expected to result in increased net photosynthesis and biomass accumulation, or in other words faster growth (Wertin 2010) along with improved water-use efficiency and improved tolerance of low photoperiodicity (Drake *et al.* 1997; Norby *et al.* 1999; Nowak *et al.* 2003). Assimilation of CO_2 during photosynthesis is the key to plant metabolism (Taub 2010). Studies show that plant growth and yield can increase by 30% or more with doubling CO_2 concentration (Kimball *et al.* 1993). Elevated atmospheric CO_2 concentration increases the photosynthesis rate on average by about 40% and accelerates plant growth. The dry matter produced in plants grown under free air CO_2 enrichment increased by 17% for the above-ground and more than 30% for the below-ground portions of the plant (Ainsworth and Rogers 2007). Other studies (Egli *et al.* 1998; Würth *et al.* 1998a,b; Granados and Körner 2002; Körner 2006) however, argue that there is little evidence to support claims that elevated CO_2 levels will influence tree growth.

2.6.4 Fires

With the expected increase in temperature and decrease in precipitation, the occurrence of wild fires in Southern Africa can be expected to increase. Fire intensity significantly depends on fuel availability, wood moisture and prevailing weather conditions (Cheney *et al.* 1998). Damage of the cambial and sapwood region, as well as defoliation following crown scorch contribute to changes in tree growth (Bond *et al.* 1994; Odhiambo *et al.* 2014). The reaction of trees to fire is not only reflected in the area exposed to the fire but is also reflected systematically in the ring width of the stem (Schweingruber 1993). Though different species exhibit different fire-resistance mechanisms (Odhiambo *et al.* 2014), growth reduction can occur in some species following high intensity surface fire damage (Odhiambo *et al. in press*). A clear link has been found between the fire intensity, effect on the crown, regeneration and growth rates in Miombo trees (Ryan and Williams 2011).

2.7 Effect on Tree Growth

Change in climatic variables affects tree growth indirectly by affecting physiological process (Schweingruber 1996; Kozlowski and Pallardy 1997; Reape and McCabe 2008; Aroca 2012; Rötzer *et al.* 2012). The effects of climatic variables on tree growth are summarized in Table 2.1.

Table 2.1: Summarised tree responses to increase in climate variables

Physiological processes	**(Elevated) Climate characteristic**		
	Aridity	Temperature	CO_2 concentration
Photosynthesis	Declines	Inhibited	Increases (up to a point)
Respiration	Increases	Increases	Increases
Enzyme activity	Increases	Declines	
Water/mineral absorption	Modified	Higher water loss	Increases
Translocation of growth regulators	Declines	Declines	increases
Growth	Impaired	Retarded	Increases
Biomass accumulation	Reduced	Reduced	Increases
Cell and tissue	Damage/death	Damage/death	

2.7.1 Wood Anatomy

The sensitivity of species and individual trees to environmental changes manifests itself in the wood properties. Wood quality is defined by different properties and varies with the intended end use. Jozsa and Middleton (1994) and Zhang (2003) state that a small change of the wood properties affects the processing parameters and the properties of final products. Empirical evidence shows that environmental factors influence wood quality significantly (Naidoo *et al.* 2007). A good understanding of the expected wood quality is therefore essential to the wood processing industry.

The most commonly used properties to define wood quality are wood density, uniformity of growth rings, fibre length, earlywood to latewood ratio and fibre to vessel ratio, which can be quantified with high accuracy and precision (Grabner *et al.* 2006; Barnett and Jeronimidis 2009). Punches (2004) states that although ring width was used as a predictor of density, the density of wood is determined by the proportions of earlywood and latewood within a ring. Differences in the density of hardwoods stem mostly from differences in fibre and vessel properties (Shmulsky and Jones 2011; Tsoumis 2013). For most end-use applications, high density translates into high-quality wood (Jozsa and Middleton 1994).

Louw (1997) and Naidoo *et al.* (2007) assessed the effect of site characteristics on growth and properties of *Eucalyptus grandis* in South Africa and found positive correlations between site conditions and the resulting tree growth and wood anatomical properties. Naidoo *et al.* (2007) found

significant correlations between MAP and fibre and vessel characteristics. Baas and Wheeler (2011) describes the secondary xylem as multifunctional, complex plant tissue that provides an archive of the external signals that modified its functional attributes at different timescales. Several researchers reported significant correlation of water availability with anatomical features (Polge and Keller 1968; February *et al.* 1995; Corcuera *et al.* 2004; Zweifel *et al.* 2006; Naidoo *et al.* 2007; Sass-Klaassen *et al.* 2007; De Micco and Aronne 2012b). At anatomical level, reduced aridity is expected to result in shorter fibre length, larger fibre diameter, thinner cell walls, larger lumen diameter, higher earlywood ratio and wider ring. Elevated temperatures affect wood properties by increasing aridity and evapotranspiration (Dobbertin *et al.* 2010; Eilmann *et al.* 2011). Naidoo *et al.* (2007) did not find any correlation between MAT and any of the wood properties studied.

Table 2.2: Summarised effects of climatic variables on the wood anatomical structure

Wood properties	**(Elevated) Climate characteristics**	
	Temperature	Precipitation
Density (g/cm^3)	Higher	Lower
Fibre diameter (µm)	Smaller	Larger
Cell wall thickness (µm)	Thicker	Thinner
Lumen diameter (µm)	Smaller	Larger
Ring width (µm)	Narrower	Wider
Vessel freq. (No/mm^2)	Higher	Lower
Vessel coverage (%)	Higher	Lower
Vessel diameter (µm)	Smaller	Larger

2.8 Need for Future Research

A strong relationship between tree growth and climate, particularly water availability and temperature, has been found in several studies (Schweingruber *et al.* 1988; Borchert 1994; Briffa 1994; Lindholm and Eronen 2000). In studies on Brachystegia spiciformis (Trouet *et al.* 2001, 2010, 2012) and on *Burkea africana* and *Pterocarpus angolensis* (Fichtler *et al.* 2004), growth response to rainfall was found to be positive, but no significant correlation with temperature was found. Trouet *et al.* (2012) in their study on *Brachystegia spiciformis* found that cambial activity starts long after the beginning of the rain season, and the production of new xylem cells stops just before the end of the rain season. With reduction in water availability, the productivity of the trees in the seasonally dry Miombo woodlands could decrease, especially in the warmer and drier zones. Some trees will be able to cope better with climate-induced stresses than others. Due to reduction in stomatal conductance—a drought-avoidance strategy—reduction in net primary production in forest stands could occur.

Currently, the response of sub-tropical trees to climate variability is poorly understood. It is not clear whether tree growth can be expected to increase due to CO_2 fertilisation and if this would cause a depletion of soil nutrients. The rapid growth can be expected to affect wood quality of the wood and performance of the products. A detailed analysis of the growth characteristics of selected Southern African wood species, which are commercially used, will be carried out to correlate the effect of the expected climate change to the wood quality.

To achieve this, fundamental knowledge of the effect of different environmental variables on the growth of the selected species is necessary. Once the growth response is known it will be possible to predict how the growth pattern and wood quality are likely to react to the predicted climate change.

Chapter 3 Materials and Methods

3.1 Sampled tree species and woodland ecosystems

3.1.1 Sampled tree species

The three dominant Miombo tree species, *Brachystegia spiciformis* Benth, *Burkea africana* Hook and *Isoberlinia angolensis* (Benth.) Hoyle and Brenan, were selected for the study. They belong to the family of *Leguminosae*, sub-family of *Caesalpinioideae*. Apart from their economic value (Dyer *et al.* 2016), the three species were selected for this study based on their dendrochronological potential (Trouet *et al.*, 2001, 2012; Fichtler *et al.*, 2004; Syampungani *et al.*, 2010), distribution across the climate zones (Storrs 1979) and comparative ease of coring.

Brachystegia spiciformis, which varies in size due to differences in levels of water availability and growth conditions from small to large trees (up to 35 to 40 m tall), can be either deciduous or semi-evergreen. It has a stem that can be straight and cylindrical or poorly formed, with bole heights of up to 15 m and diameters up to 120 cm. Growing at altitudes of up to 2000 –2350 m, *Brachystegia spiciformis* is characteristic of the Miombo woodlands and can be found on a variety of soils. The species occurs in both coastal and upland deciduous woodland and open forest. *Brachystegia spiciformis* is found in areas receiving a mean annual rainfall ranging from 500 mm to 1200 mm. In higher rainfall areas, it often dominates the canopy (Brummitt *et al* 2007; Oyen and Louppe 2012; Palgrave and Palgrave 2002).

Burkea africana is a deciduous, small to medium-sized tree that can reach 20 m in total height. The species can have bole heights of up to 7 m and diameters up to 80 cm. It occurs in deciduous woodlands and the wooded savanna alike, at altitudes of 50–1750 m. *Burkea africana,* which is found on light, well drained soils, grows in areas receiving between 1000- and 1200-mm annual rainfall. It is usually found on loose, sandy or loam-clay soils (Bolza and Keating 1972; Brummitt *et al.* 2007; Maroyi 2010).

Isoberlinia angolensis occurs in deciduous woodlands and open forest and forms a shrub or small to medium-sized tree with a total height of 20 m. Bole heights can reach 7 m with diameters up to 50 -100 cm. *Isoberlinia angolensis* occurs on muddy, lateritic or gravelly soils. It grows at an altitude of 600-2100 m, often gregariously. It grows either as a dominant or co-dominant species (Brenan 1963; Brummitt *et al.* 2007; Handavu *et al.* 2011; Oyen 2012)

3.1.2 Wood properties and uses

The three selected tree species are an important source of timber for a variety of products. The wood of the three species is used in Zambia for heavy construction, as parquet flooring, as railway sleepers, as poles and for furniture and joinery. It also finds use in the production of mine props and as firewood and charcoal in smelting copper (Dyer *et al.* 2016; Maroyi 2010; Oyen 2012; Oyen and Louppe 2012). The wood from the sample species has also been used in the production of sports equipment and musical instruments, for interior trim, vehicle bodies, making of door frames, canoes, utensils, boxes, crates, veneer and plywood, and in the paper production.

Some of the mechanical properties of the wood from the three species are summarized in Table 3.1

Table 3.1: Mechanical properties of the sample species (Source: Dyer *et al.* 2016)

Property	**Species**		
	Brachystegia spiciformis	*Burkea africana*	*Isoberlinia angolensis*
Density (12% MC) (Kg/m^3)	680–915	735–1020	820 kg/m³
Shrinkage (Green to Oven Dry)			
Radial	2.9–4.1 %	2.9–5.6%	5,60%
Tangential	4.3–5.8 %	4.2–9.2% t	6,90%
Modulus of rupture (MOR) (12% MC)	88–125 N/mm²	84–143 N/mm²	
Modulus of elasticity (MOE) (12% MC)	11,100–14,400 N/mm²	12,940 N/mm²	
Compression parallel to grain	60–69 N/mm²	48–85 N/mm²	
Compression perpendicular to grain		12 N/mm²	
Shear strength	11–16 N/mm²	14.5–15 N/mm²	
Cleavage	15–16 N/mm		
Janka side hardness	6620–8140 N	6490 N	
Janka end hardness	6850–7920 N	7605 N	

Brachystegia spiciformis wood has no strong natural durability and preservative impregnation, even under pressure, of its heartwood is difficult. However, Oyen and Louppe (2012) advise that the use of prolonged pressure ensures satisfactory impregnation of the sapwood. Chipping difficulties and low pulp yield make the wood unsuitable for paper production (Oyen and Louppe 2012).

Though not difficult to saw, the wood of *Burkea africana* is hard and difficult to work on with hand tools. The presence of interlocked grain makes it susceptible to tearing when planning. It turns well and has good finishing and gluing properties. Splitting makes pre-boring prior to nailing necessary. While its sapwood is more permeable, preservative treatment of the heartwood of *Burkea africana* is very difficult (Maroyi 2010).

Isoberlinia angolensis wood can be worked with moderate ease using machine tools but is difficult to work with hand tools. When using hand tools, considerable blunting on tool edges occurs. During planing, the grain tends to pick up. The wood has good gluing properties but does not turn well. It has moderate durability. Both its heartwood and inner sapwood resist preservative impregnation, but its outer sapwood is permeable (Oyen 2012).

3.1.3 Woodland ecosystems

Zambia is divided into seven ecoregions (Fund 2011; Malambo and Syampungani 2008) and samples for this study were obtained from two ecoregions: the central Zambezian Miombo woodlands and the southern Miombo woodlands. Campbell (1996) described the Miombo woodlands as the most extensive tropical seasonal woodland and dry forest formation in Africa. The woodlands, which occur on nutrient-poor soils, cover an area about 2.7 million km^2 (Campbell 1996). They occur in regions that receive a mean annual rainfall ranging from 650 – 1400 mm (White 1983) and are characterised by a 5-7 months long dry season (Frost 1996). Miombo woodlands are dominated by trees of the genera *Brachystegia*, *Julbernadia, Isoberlinia, Baikiaea*, *Cryptosepalum*, *Colophospermum* and *Burkea (Fabaceae,* subfamily *Caesalpinioideae)*. In Zambia, Miombo woodlands, covering 65% of the country, are the most widespread of the woodlands (Malambo and Syampungani 2008). Based on differences in mean annual rainfall received, White (1983) divided the Zambian Miombo into two subtypes: the drier (<1000 mm) and wetter (> 1000 mm) Miombo.

Zambian forests are further classified into closed forest, open forest, grassland with bush, and grassland. Trees in the closed forest group have two phenology classes: evergreen, with a high stature class (tree heights >10 m) and deciduous, with a low (tree heights <10 m) thicket stature class. Open forest trees are deciduous, with a high (5-15 m) stature class (Forestry Department 2016). Most of the species in the Miombo woodlands of Zambia are deciduous (Forestry Department 2016; Trouet *et al.* 2012), which is a reflection of the adaptation of their eco-physiology to climatic and site conditions (Forestry Department 2016). The Miombo woodlands are rated one of the forest ecosystems, which are most threatened by overexploitation, deforestation and climate change impacts (Makonda and Gillah 2007; Syampungani *et al.* 2009; Jew *et al.* 2016; Gonçalves *et al.* 2017).

3.2 Study sites

Sample material was collected from sites in natural forests. According to Forestry Department (2016), natural forests cover circa 61% of Zambia's total land area (752, 000 km^2). Of these, 7.2 million ha (180 National Forests covering 5,145,162 hectares or 6.8 % and 307 Local Forests covering 2,076,062 hectares or 2.8 %) fall under the control of government and are designated as protected forest areas under the Forests Act No. 4 (2015) of the Laws of Zambia. Study sites were

selected to cover a large geographic area and all climatic zones. The general location of the study sites is shown in the map of Zambia in Figure 3.1.

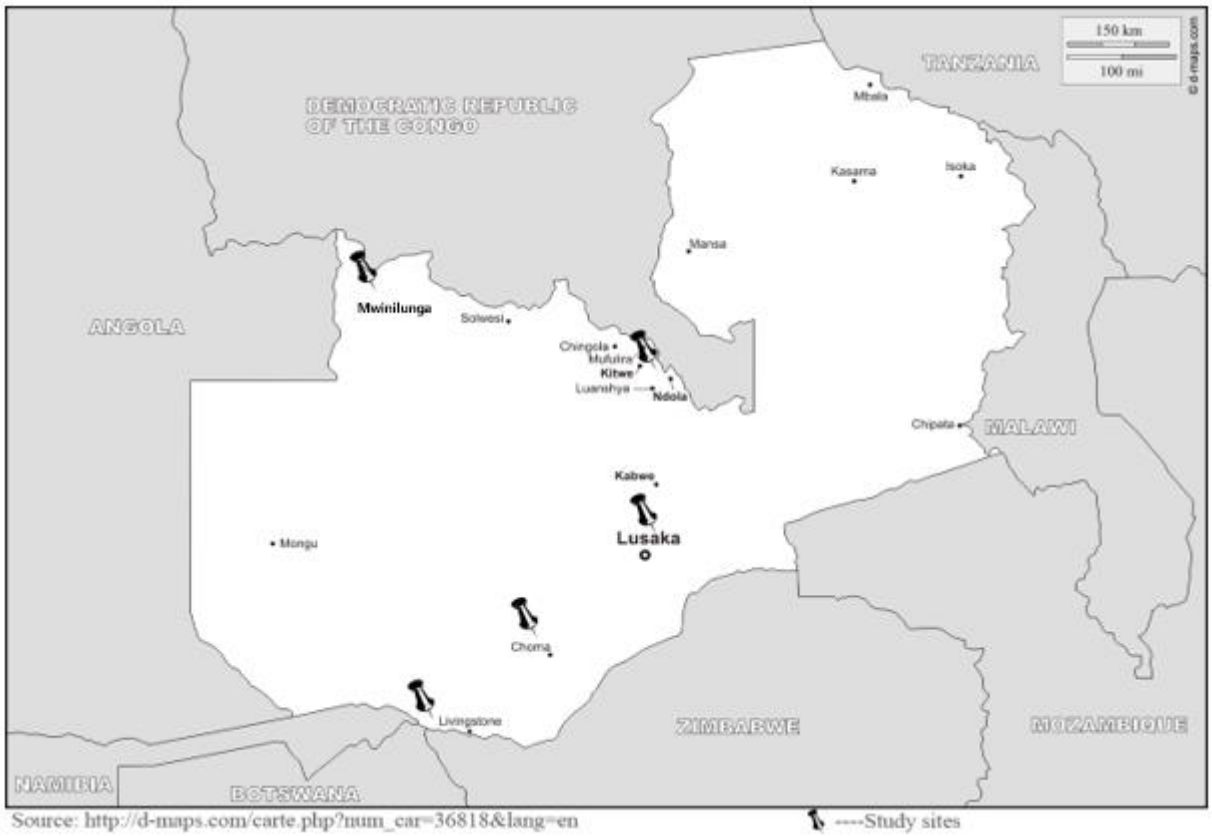

Figure 3.1: Map of Zambia and the location of study sites

Sampling was done from the following forest reserves: Simoonga F.67 (Livingstone), Lusaka F.27 (Lusaka), Choma F.46 (Choma), Mwekera F.6 (Kitwe), Masansa F.3 (Mufulira), and Luakera River F.74 (Mwinilunga). Depending on location, the sites differ in terms of stand density. An assessment by the Forestry Department (2016) found that the forest reserves in high rainfall areas (Central Zambezian Miombo woodlands) have a higher mean density (231 trees/ha) compared to those found in the low rainfall (Southern Miombo woodlands) areas, which have a lower mean density (128 trees/ha).

Zambia has a climate which, depending on altitude, is either tropical or subtropical. The climate is divided into a rainy season (November to April), a dry season (May to October/November) and a hot, dry season (September to October/November) (McSweeney *et al.* 2008; Eroarome 2009). Mean monthly temperatures across Zambia ranges from as low as 5ºC (in winter) to 30ºC in summer. In the last four decades, there has been an increase in inter-annual rainfall variability and a decrease in annual precipitation (Gannon *et al.* 2006; Kirtman *et al.* 2013). Due to the prevalence of relatively

high temperatures in Zambia, potential evapotranspiration often exceeds precipitation resulting in the country being left with a soil moisture drought (GRZ 2007).

Based primarily on mean annual precipitation (MAP), Zambia is divided into three agro-ecological zones, shown in Figure 3.2 (Eroarome 2009). The zones were designated using the “FAO length of growing period model” (FAO 1978), a tool used to assess agricultural resources and potential (Fischer *et al.* 2012). The classification into AEZs also takes in account soil type and other climate characteristics.

To understand the effect difference in site conditions has on the growth of the studied tree species, sites (indicated by four-point stars in Fig. 3.2) representing the range of growing conditions across the zones were selected. The sites in each zone exhibit similar climatic conditions. For agricultural purposes, these are conditions that determine an area’s ability to support rain-fed agriculture (Harvest Choice 2010) as well as other socially valuable non-food goods and environmental services (Fischer *et al.* 2012; Henricksen 1986).

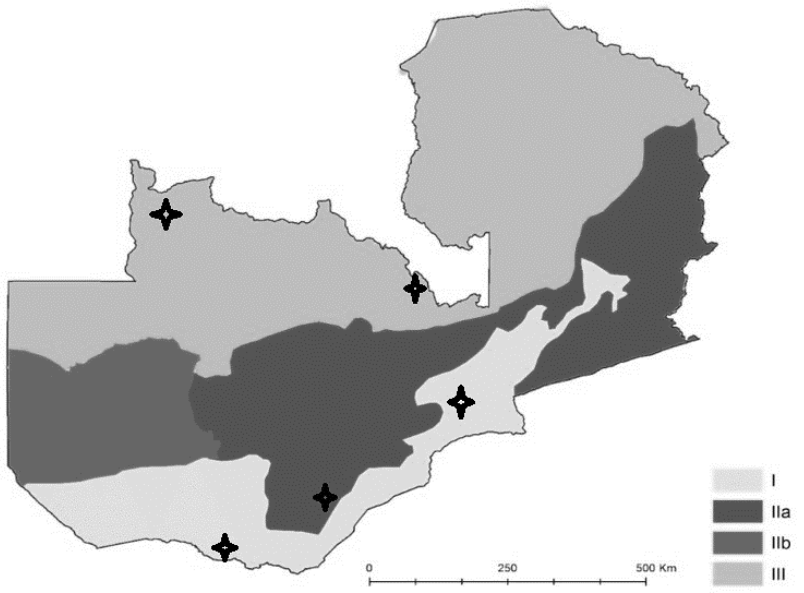

Figure 3.2: Map of Zambia with agro-ecological zones (Source: Dept. of Meteorology Zambia).

Land is classified into agro-ecological zones based on factors such as soil distribution, land surface and climate (FAO 1996). Apart from seasonality, factors, such as latitude, elevation, and temperature influence AEZs (HarvestChoice 2010). Other factors are distribution and amount of rainfall during the growing season.

AEZ I:

Accounting for circa 15% of the country's total land area, AEZ I covers Zambia's major valleys. Most of the major rivers pass through this zone, which lies at an altitude below 1,000m above sea level. Poor, sandy soils limit its agricultural potential. MAP for AEZ I is <800 mm. In this zone, poorly distributed rain and frequent dry spells increase the risk of drought. The zone has a relatively short (80-120 days) growing season. With higher temperatures than in the rest of Zambia, AEZ I has the harshest climatic conditions (GRZ 2007).

AEZ II:

This zone crosses the middle of Zambia from west to east. Plains, plateaus and a mountain range are part of this zone. Its elevation ranges from 1,000 to 1,400 m above sea level. The zone is characterised by a growing season of 120-160 days, with a MAP of 800 – 1000 mm. Rainfall distribution is not as erratic as in AEZ I, though dry spells occur frequently. AEZ II, with an area of 27.4 million ha, is further divided into two sub-zones: IIa and IIb. AEZ IIa covers the central, southern and eastern plateaus. With fertile soils, it has the best agricultural potential of all the zones and has abundant, perennial water sources. IIb has similar rainfall patterns as Zone IIa, but is characterised as semi-arid plains, because of a different soil type. The soils found in this zone are mostly sandy and less fertile compared to those in IIa. This zone's production potential is reduced by high temperatures (GRZ 2007).

AEZ III:

Forming part of the central African plateau, AEZ III is the largest of the three zones (40.6 million ha). AEZ III receives a MAP exceeding 1,000 mm and has a long growing season (>160 days). Zone III has soils that are highly weathered and leached and which are characterized by extreme acidity (GRZ 2007).

For purposes of this study, sites with reliable climate data were identified and selected. Each of the study sites in Livingstone, Kitwe, Mufulira and Choma are less than 10 km from the corresponding weather station. Only the sites in Mwinilunga and Lusaka were located between 10 and 45 km from the nearest weather station. Precipitation and temperature data in the form of monthly totals for the period 1980-2014 were obtained from the Zambian Meteorological Department. The data were analyzed to obtain means of precipitation and temperature for each site, which were then used to characterize the sites based mainly on their aridity indices. Aridity indices provide an estimate of the amount of water available in the soil at a location. Aridity can be assessed in different forms such as a precipitation-effectiveness index (Thornthwaite1948), index of aridity (De Martonne 1925), the UNESCO (1979) $P/ET_{o\text{-}PM}$, or as an aridity coefficient (Gorczynski 1940). The aridity was, in this study, described using De Martonne's aridity index ($I_{ar\text{-}DM}$), which has comparably low meteorological

data requirements and is therefore simpler to calculate (Paltineanu *et al.* 2007). De Martonne's aridity index (DMI) is determined using Equation 1:

$$DMI = \frac{P}{T+10} \quad (1)$$

Where P is the mean annual precipitation (mm) and T is the mean annual temperature (ºC).

Using De Martonne's global aridity classification, sites are generally classified into very dry (0-5), dry (5-15), semi-dry (15-20), mildly wet (20-30), wet (30-60) and very wet or humid (>60) (Botzan *et al.* 1998; HOA 2012). The characteristics of each of the sampled sites are summarised in Table 3.2.

Table 3.2: Study site characteristics

	Livingstone	Lusaka	Choma	Kitwe	Mwinilunga
Zone	I	I	II	III	III
Site location	17°49S	16°49S	15°25S	12°36S	11°45S
	25°49E	27°30E	28°27E	28°70E	24°26E
Elevation (m)	986	1278	1280	1243	1361
MAP (mm)	697	802	806	1293	1332
Max_MAT (°C)	31	27	27	29	28
Min_MAT (°C)	14	15	13	11	13
DMI	15	20	21	33	35
DMI Class	Dry	Semi-arid	Mildly wet	Wet	Wet

Differences in aridity give rise to study sites that range from dry (Southern Miombo woodlands) to wet (Central Zambezian Miombo woodlands). This is shown in Table 3.2 and illustrated in Figure 3.3a and b. The variations are based on mean values and a confidence level of 95%. Although they show differences in MAP and MAT, the study sites have a similar mean photoperiod (circa 12 hours) and similar soil characteristics. Across the sites, the soil was found to generally consist of ≃ 10% clay, 4% silt, and 86% fine sand, which is classified as either sandy or sandy-loam. Between sites in Zones I and II, the differences in MAP and the mean December-February precipitation (the core of the rain season in Zambia) are insignificant ($p>0.05$). However, MAP and December-January-February (DJF) precipitation differ significantly ($p<0.05$) between sites from Zones 1 and 2, when compared to those in Zone 3, as displayed in Figure 3.3a.

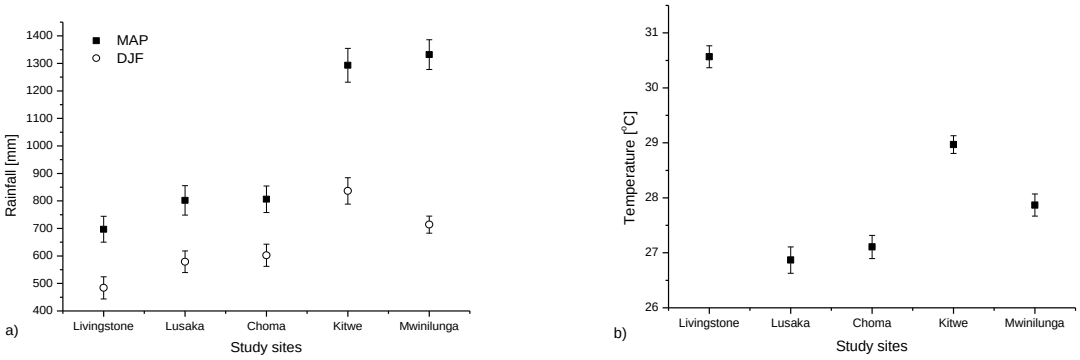

Figure 3.3: a) Rainfall for the entire year and rainy season and b) temperature variation within and between sites

GRZ (2010) reports that each AEZ received below normal rainfall in 10 out of 14 years between 1990 and 2004. As shown in Figure 3.4, significant variability in rainfall, influenced by the movement of the Inter-Tropical Convergence Zone (ITCZ) and El Niño/Southern Oscillation (ENSO), is a common feature of the climate in Zambia (GRZ 2007, 2010a).

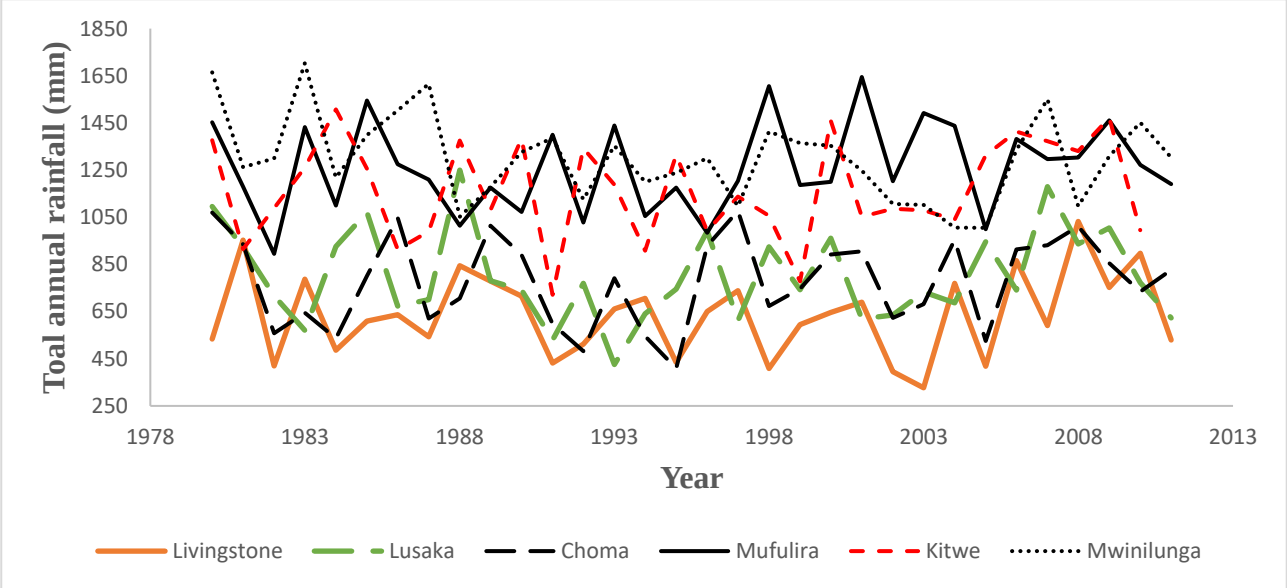

Figure 3.4: Rainfall variability in the study sites

For each of the sites, year-on-year variability of rainfall for the base years 1980-2012 is illustrated using total rainfall (Figure 3.4) and rainfall indices (Figure 3.5). The indices reflect the amount of precipitation received at each site relative to the long-term average for the site and timeframe indicated.

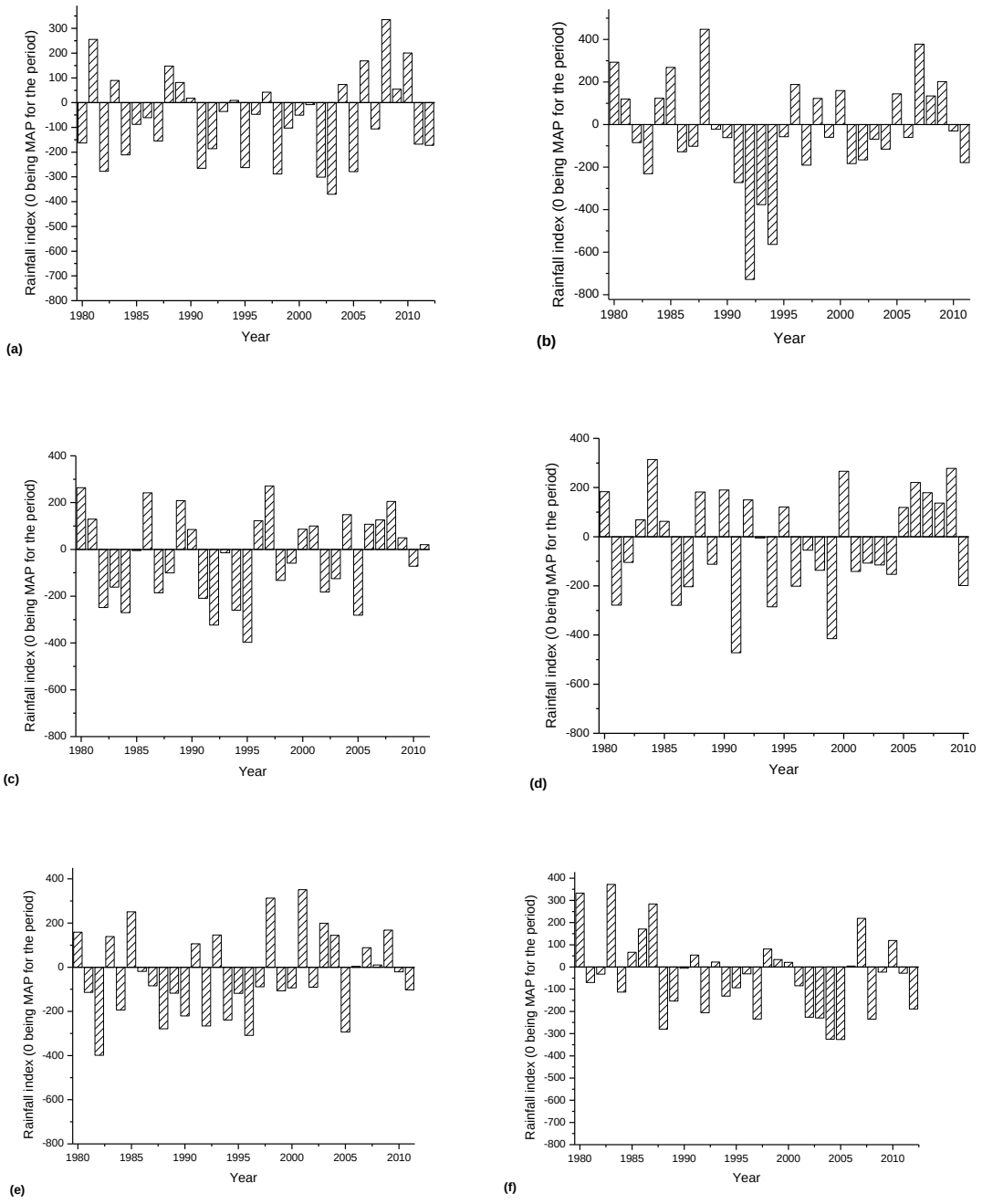

Figure 3.5: Rainfall indices averaged over site a) Livingstone, b) Lusaka, c) Choma, d) Kitwe, e) Mufulira and f) Mwinilunga

An example of the trees in a low rainfall area is shown for Lusaka in Figure 3.6.

Figure 3.6: Miombo woodland on a dry site during the dry season

About 80% of Zambia lies on a plateau between 1,000 and 1,500 metres above mean sea level and temperatures are affected by this altitude and therefore lower, compared to the coastal areas at the same latitude. The temperature ranges for Zambia are as shown in Table 3.3

Table 3.3: Mean annual temperature variation across the seasons (GRZ 2010b)

Months	Season	Mean Daily Maximum (°C)	Mean Daily Minimum(°C)
May - Aug	Cool and Dry	21-26	6-12
Sept-Oct	Hot and Dry	28-35	17-22
Nov-April	Rainy	25-30	14.19

Seasonal variations in temperature are large. Temperatures range from highs of 23-31°C during the day to night time temperatures as low as 5°C. The Luangwa and Zambezi valleys typically experience day time temperatures as high as 40°C during the hot and dry season (GRZ 2010b,a). Rainfall has a cooling effect on temperature during the rainy season. Among the study sites, Livingstone, which has the lowest MAP also has the highest MAT. Lusaka and Choma – rated “dry” to “mildly wet” according to the DMI – had comparably low MATs, followed by Mwinlunga and Kitwe (wet sites).

3.3 Sampling procedure

For at least 15-20 trees per species at each of the sites located along a precipitation gradient purposefully selected through visual inspection, the following tree variables were determined: diameter at breast height (DBH), total height, bole height (the height up to the lowest or first live

branch), and crown diameter. To obtain a long history from each site, large trees were targeted. Care was taken to avoid trees with obvious reaction wood (by avoiding leaning stems, for example) and other defects (e.g. visible stem rot). Because of the possible edge effect on a variance in growth rate, trees on the edges of the forest were avoided. Research has shown that the edge and interior of a stand are contrasting habitats (Kacholi 2014).

Crown diameter was determined by first measuring radii in four cardinal compass directions using a plummet (Pretzsch *et al.* 2015). The surveyor measured the distance (in m) from the centre of the tree trunk to the branch tip in each of the four directions using a distance tape. The mean of two diameters (N-S and E-W) was taken as the crown diameter. The stem diameter at breast height (1.3m) was measured in centimetres with a diameter tape (D-tape), while height (in m) was measured using a combination of a Hypsometer (Vertex IV) with a ultrasonic Transponder T3 (Haglöf Sweden A.B 2007) to measure the distance. The hypsometer measures an angle to the tree tip and calculates the tree height trigonometrically, based on the measured angle and the distance to the tree received from the transponder. Typical accuracies of those measurements are in the range of ± 0.1m. For each tree, mean values, with error bars representing 95% confidence intervals, of diameter measured at breast height (DBH, 1.3 m), total tree height (m) and age (years) were calculated and plotted. Analysis of variance and a Tukey Highly Significant Differences (HSD) test were then used to make inferences about the statistical significance at 0.05% probability level of the obtained mean values.

The study made use of tree cores, as a non-destructive method of sampling. This allowed the study of quite a sizable sample size of trees, without the cost of losing several trees by cutting them down. At each of the sites, 2 cores per tree were removed from breast height (1.3 m) at 90 and 180 degrees to the main wind direction using a 5-mm increment borer (as shown in Figure 3.7). Collecting increment cores from as close to breast height (Trouet *et al*. 2006) avoided the problem of wedging rings associated with the base of a stem.

Figure 3.7: Coring *Brachystegia spiciformis* in one of the forest reserves found in Southern Miombo woodlands

For trees with thick bark, the auger (drill) was removed from the increment borer handle and attached to a Makita 18V Cordless Impact Driver (Makita Power Tools SA 2015). The driver was then used to power the auger into the bark, after which the driver was removed, and the auger re-attached to the increment borer handle. Then drilling into the wood continued manually.

After collection, each of the cores was labelled to indicate the site, species, tree number, and core number, after which it was placed in a sample holder.

At each site, a soil sample was collected using a stainless-steel soil auger. The samples were taken from a depth of 0.20 m. An equivalent of 800 grams of the soil from each site was placed in a marked plastic bag, sealed and later sent to a soil testing laboratory (Bemlab) for analysis.

The key variables analyzed were soil pH, volumetric stone percentage, resistance (indication of soil salinity), phosphorus, potassium, organic carbon and soluble Sulphur content. Furthermore, mechanical analyses were conducted to classify the soil type based on clay, silt and sand percentages.

3.4 Sample preparation and tree-ring analysis

After collection, standard procedures for preparing core samples, as outlined in Grissino-Mayer (1999) and Speer (2010), were followed. The cores were dried, after which they were placed in a wooden mount with the fibres oriented vertically, and then sanded in preparation for ring analysis. The cores were sanded starting with a coarse grit (size 100) sandpaper and then progressively polished with finer sandpaper (up to grit-1200), until the ring boundaries were clearly distinguishable, as shown in Figure 3.8.

Figure 3.8: Sanded cores on a wooden mount

After sanding, the tree-ring boundaries were detected under a stereo microscope and measurements (to the nearest 0.01mm) carried out using LINTAB equipment fitted with a Time Series Analysis and Presentation (TSAP) software (Rinn 2013). Two cores from each tree were then cross-dated. A combination of visual and statistically aided cross-dating was used. The aim of the cross-dating was to see if trees of the same species growing under the same site conditions produced a comparable pattern of wide and narrow rings. For the statistically aided cross-dating TSAP selects many data stacks and automatically calculates several statistical parameters for the matching positions and sorts them according to the highest relevance. After cross-dating an average tree curve per species and site was created. The equipment used for tree-ring measurement is shown in Figure 3.9.

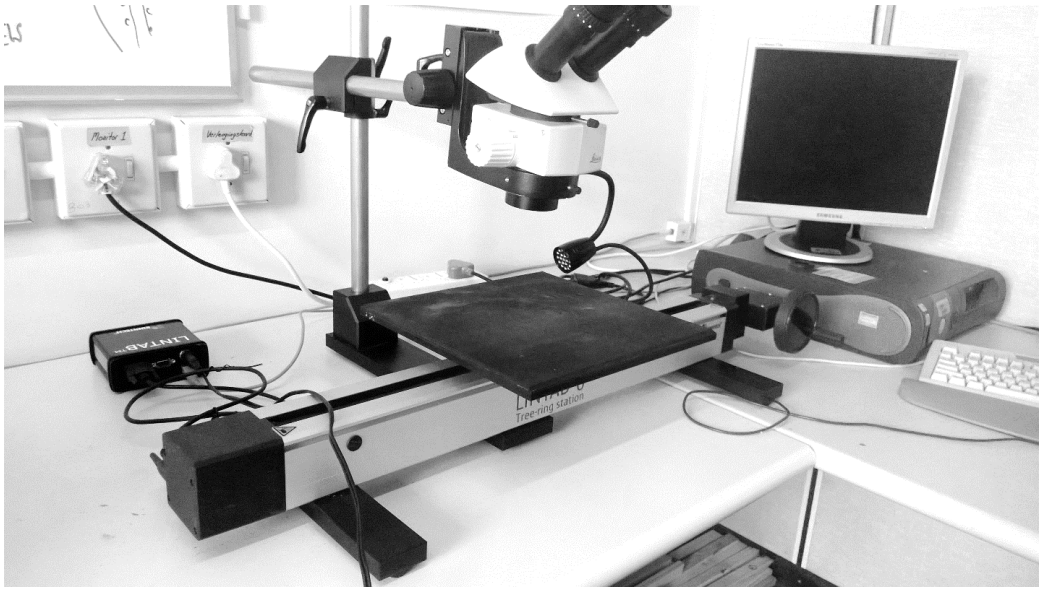

Figure 3.9: LINTAB 6 Tree-ring station

3.5 Data analysis

Origin 8.5.1 was used for statistical analysis and mean values with error bars, representing 95% confidence intervals were plotted. Analysis of variance and a Tukey honest significant difference (HSD) Test were used to test the statistical significance at a 0.05 % probability level of the mean values. To understand the relationship among the variables, correlation analysis was conducted.

Statistical analysis of the sequences of the tree-ring widths for all the measured trees was performed with TSAP. Cross-dating was done statistically by calculating the Student's *t*-value and *Gleichläufigkeit* (GLK) value (Baillie *et al.* 1973). GLK measures the percentage of years, where the two-compared time-series show identical growth patterns. For each of the species, a cross-dating threshold like the one used by Trouet *et al.* (2010) was applied, consisting of a t-value of 2 ($p<0.05$) and a GLK of 60%. Cross-dating success varied between sites. On the dry sites (Livingstone, 10; Lusaka, 10; Choma, 9) higher cross-dating success was achieved. In trees from the wet sites, crossdating was possible in 8 trees for *B. Spiciformis*, and in 7 for *Isoberlinia angolensis and Burkea africana***.** Crossdating difficulties were encountered in *Isoberlinia angolensis*, where ring boundaries in some samples became indistinct towards the pith.

In trees, ring widths tend to decline with age. In dendrochronological studies, there is need to estimate and remove this age-related trend to remain with evidence of climate effect (Melvin & Briffa 2008). Detrending removes the expected ring-size at each age if there was no variation in climate. After cross-dating, ring width was plotted over time (Figure 3.12a). Linear, logarithmic, exponential and polynomial functions were then fitted to the data, with the cubic (polynomial) function being found to be the most appropriate function for removing the age-effect as it optimally fit the data. Fitting a polynomial function to the RW data removed the age effect and hence allowed focus on data fluctuations which could be attributed to differences in growth conditions. The function $Y = A+B\cdot x+C\cdot x^2+D\cdot x^3$ was used to fit the RW data. Where, Y stands for the resulting residual RW, x represents the year and A, B, C and D are the fit parameters. The residual ring width is plotted against time as shown in Figure 3.10b.

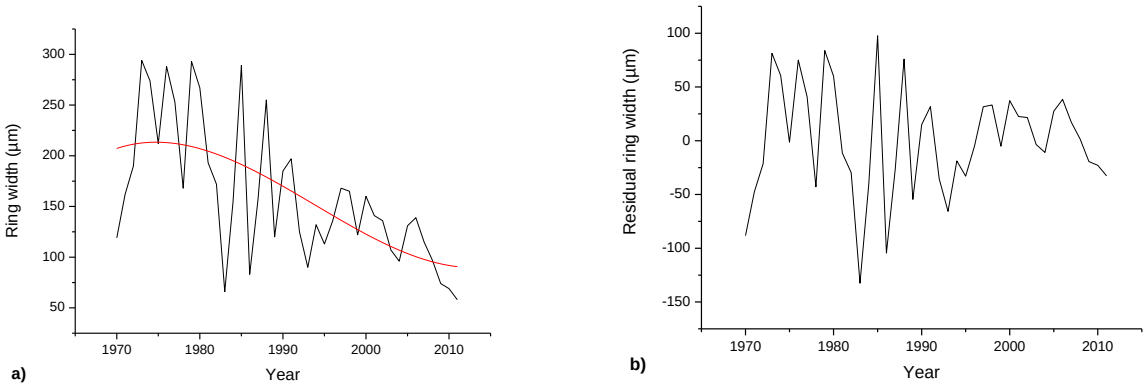

Figure 3.10: Ring width a) prior to detrending and b) after detrending

The example given in Figure 3.10 is for *Brachystegia spiciformis* from a dry site (Lusaka).

Further statistical analysis to determine the interactions between the species and their environment was performed with Origin (version 8.5.1). The correlation coefficients for ring width and DMI, MAP and MAT, respectively were calculated for each species and site, to show the influence of water availability and temperature on tree growth. Furthermore, the correlation between the mean sensitivity and DMI was determined.

The mean sensitivity, which Douglass (1936) defined as the "mean percentage change from each measured annual ring value to the next," was calculated using Equation 2:

$$MS = \frac{(X1-X2)}{(X1+X2)/2} + \frac{(X2-X3)}{(X2+X3)/2} \ldots\ldots \quad (2)$$

Where X1 is the most recent year's growth (in cm), X2 is the previous year's growth and X3 is the growth that took place the year before X2, etc. until all the rings are accounted for.

The site-specific sensitivity of each species to fluctuations in environmental factors was compared to gain better understanding of the response of each species to variations in water availability or temperature.

For each species, analysis of variance was carried out to test if the effects of site conditions on tree growth were statistically significant.

The variance of each RW time series was calculated using Equation 3 (Fritts 1976):

$$s_x^2 = \frac{1}{n-1}\sum_{t=1}^{t=n}(x_t - m_x)^2 \quad (3)$$

Where m_x is the mean RW, t is the growth year, with $t_{=1}$ being the earliest ring and $t_{=n}$ the last year's growth. The variance indicates the average deviation of all RW values from the mean, or in other words, the variation in RW over the years.

3.6 Sample preparation for wood anatomical studies

3.6.1 Sample selection for wood anatomical analyses

By plotting the residual ring width and DMI as a function of time in years (as illustrated in Figure 3.11), one extremely dry and one wet year - not more than five years apart, to minimize the age influence - were identified for each site and selected for the analysis of wood anatomical properties with Computed Tomography (CT) analysis. The selected years for each site are presented in Table 3.4.

Table 3.4: Data for extreme climate events.

Site	MAP (mm)	Drought year rainfall (mm)	Event Year	Wet year rainfall (mm)	Event Year
Livingstone	697	327	2003	866	2006
Lusaka	802	636	2002	946	2005
Choma	806	525	2005	1011	2008
Kitwe	1294	1000	2005	1645	2001
Mwinilunga	1334	895	1982	1545	1985

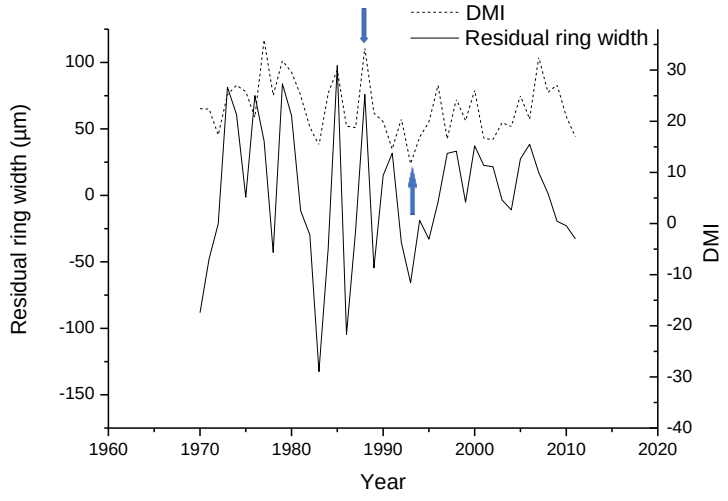

Figure 3.11: Example of ring selection for anatomical analysis

From three cores obtained from three different trees per species and site, the two identified growth rings were cut out, resulting in a total of 30 samples for *Brachystegia spiciformis* and 18 each for *Burkea africana* and *Isoberlinia angolensis*, respectively. From the original core thickness of 5 mm, all the wood sections were subsequently reduced to a thickness of about 2 mm for Nano-CT analysis using the equipment shown in Figure 3.12. Though thin sections are still much more informative than CT images, a major advantage of using CT images of wood is that a high amount of data can be generated without the time-consuming approach of microtomy.

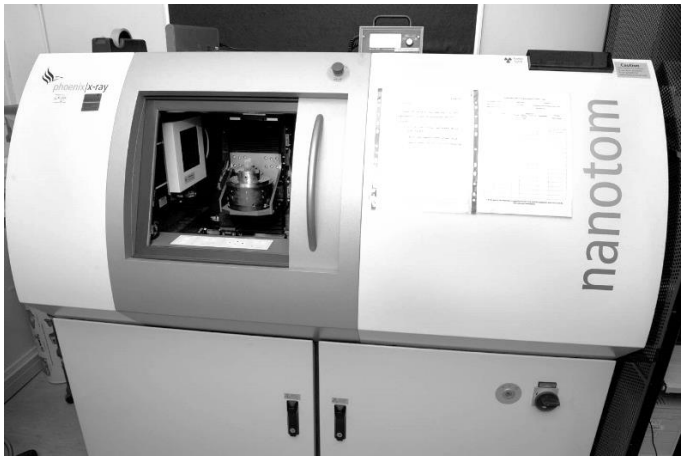

Figure 3.12: The Nano-CT scanner used for anatomical studies

Though the samples had the same thickness, their dimensions differed depending on the depth to which the cross=section was sanded and the ring width. For this reason, the region of interest (area) depended on the ring width.

The subsample was small, but by picking two extreme (dry and wet) years for the different species and sites, respectively, the subsample adequately captured the expected variability in anatomical properties resulting from water stress.

3.6.2 CT analysis

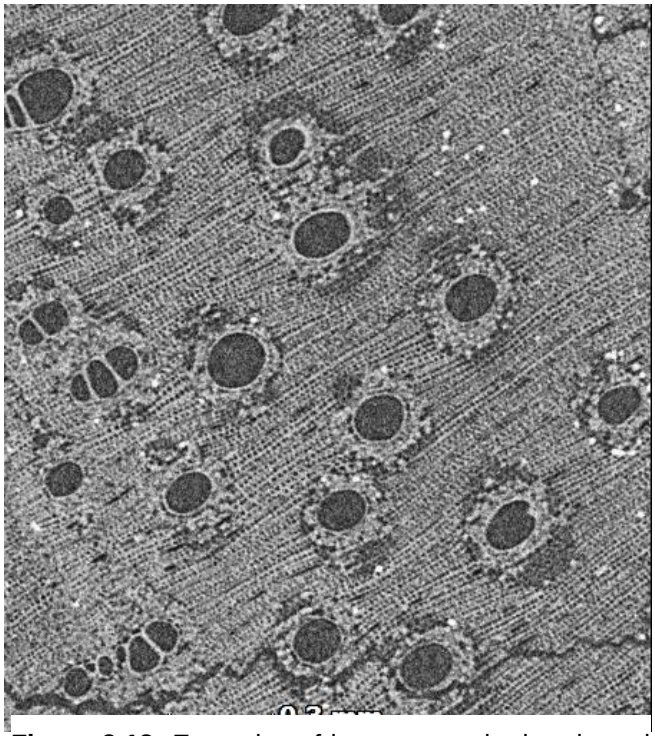

Figure 3.13: Examples of images acquired and used for VD measurements

MicroCT scans were performed with a General Electric Phoenix VTomeX L240 microCT scanner at a resolution of 2.5 µm. Image reconstruction and analysis were done using the system-supplied Datos reconstruction software, while fibre and vessel feature visualization and analysis was performed using Volume Graphics VGStudioMax 3.0 (du Plessis *et al.* 2016, 2017). Examples of images acquired and used for measurement of fibre and vessel features are shown in Figures 3.13 and 3.14. The size (area) of the region of interest, from the cross-sectional images per species per site each of the samples varied with ring size. The images were analysed for vessel frequency (number of vessels counted per unit area), vessel diameter (µm), mean vessel area (mm^2), cell wall thickness (CWT) (µm) and cell diameter (CD) (µm) measurements. Measurements were carried out in the radial direction, since differences in the tangential direction are due to genetics rather than environmental conditions. The cell diameter was determined as average of several measurements in all directions.

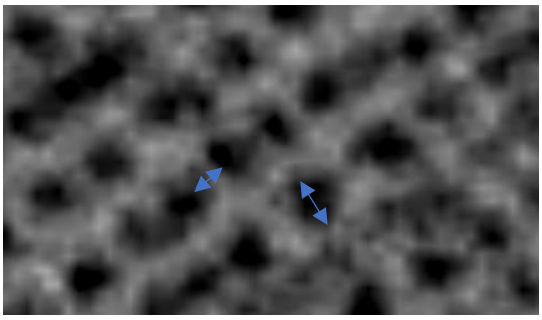

Figure 3.14: Magnified CT image used for CWT and CD measurements

Figure 3.14 illustrates how cell wall thickness and fibre diameter dimensions in the radial direction were determined. Cell wall thickness was determined as half (½) of the value of the distance between cell lumina, as this distance constitutes two neighbouring cell walls.

3.7 Statistical analysis for wood anatomical studies

The objective of the anatomical analysis was to determine the effect of climatic conditions on wood growth through the analysis of tree rings and wood anatomical properties. For this, wood anatomical

changes due to extreme climate events were analysed. Fibres and vessels from wood formed during a dry year were characterised and compared to those from wood formed during a wet year.

Simple statistical analysis was used to obtain mean values, standard deviation and standard error for fibre and vessel variables. The mean values of each anatomical property were plotted against the level of wetness and an allometric function, explaining the relationship of the two variables, fitted. A one-way analysis of variance (ANOVA) was applied to test for differences in the mean values of fibre characteristics for each of the species with site as the factor. After performing ANOVA, independent t-tests were performed, at 95% confidence level, to make inferences about the significance of differences in the mean values of cell dimensions between years and between sites. The results of the fibre and vessel measurements were graphically represented with Origin (version 8.5.1), with error bars representing 95% confidence intervals.

3.7.1 Sample preparation for ring width-density correlation

Several methods for determination of density, such as gravimetric methods, densitometry (Hamm 1995; Malan and Marais 1992), computed tomography (Rao *et al.* 1999), resistance drilling, (Gao *et al.* 2017) exist. Determination of wood density using gravimetric methods can be based on either the Archimedean principle or using densitometers. In gravimetric methods, the mass is determined (Macedo *et al.* 2002; Harvey 2008), while in radiation densitometry, the intensity of radiation that passes through a sample is measured to enable the variations in density to be automatically recorded (Cown and Clement 1983; Macedo *et al.* 2002).

In this study, the macroscopic basic wood density of selected tree rings was determined using the Diana Smith method (Smith 1954). This method, though old, is an acceptable method and is used regularly in wood science. Compared to weight-volume methods which are often used when obtaining specific density values, the Diana Smith method avoids inaccuracies and difficulties associated with volume determination when dealing with small wood samples of irregular shape. The Diana Smith method is extremely simple as it requires that the samples be first completely water-saturated and then oven-dried. The saturated and dry weight of the samples can be accurately and very easily measured. To study the effect of RW on density, 50 ring sections per species (covering all the climate zones) were cut out and numbered for ease of identification. Examples of wood sections prepared for density determination are shown in Figure 3.15.

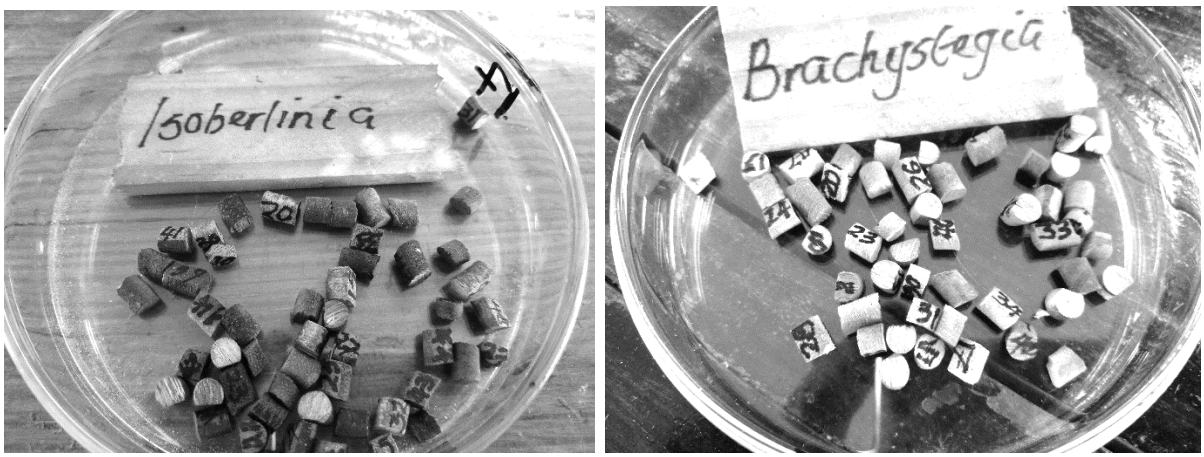

Figure 3.15: Wood sections for density determination

After being labelled all samples were put in nylon mesh bags, placed in a water tank and then subjected to cycles of over- and under-pressure for 5 days, starting with under pressure (to remove air) and ending with overpressure, to ensure a fully saturated mass. Upon removal from the tank, the saturated weight was determined, and the samples were placed in an oven for 24 h at 103°C to dry to constant mass, after which the oven-dry weight was determined and recorded. Using this method, density is determined using the relationship between maximum moisture content and specific gravity without having to directly determine the volume of the sample. Density was calculated using Equation 1:

$$\text{Density } (\text{g/cm}^3) = \frac{1}{\left(\frac{M_w - M_d}{M_d}\right) + \frac{1}{1.53}} \quad (4)$$

Where, M_w is the wet mass and M_d is the oven-dry mass of the sample.

After density determination, the effect or ring width on density was determined by plotting the density of each section as a function of RW.

3.7.2 Modelling expected changes in wood anatomy

In this part of the study, an attempt was made to describe the expected changes in wood anatomy in response to the predicted climate change using predictive modelling. Since one of the most useful characteristics of wood anatomy is that it reflects environmental conditions during wood formation, the modelling approach utilized the relationship of environmental factors and wood anatomical properties.

Expected changes were modelled using linear regression based on projected MAP values obtained from the emissions scenario RCP8.5, the model bcc_csm1_1 and the known response of the

selected wood characteristics (residual ring width, fibre and vessel characteristics) to changes in MAP. Representative Concentration Pathways (RCPs) are scenarios showing the result of different levels of greenhouse gas emissions, from the present day to 2100, on global warming (Rogelj *et al.* 2012). Four different climate change scenarios are described by the RCPs, based on different assumptions regarding population size, level of economic growth, energy consumption and the sources of this energy and how the land is used during the period of interest. In each of the four scenarios (RCP 2.6, RCP 4.5, RCP 6, and RCP 8.5), atmospheric CO_2 concentration is higher in 2100 compared to current levels (Moss *et al.*, 2008; van Vuuren, 2011; Monier *et al.* 2018)

Under RCP2.6, it is assumed that CO_2 emissions at global level will peak to around 440 ppm by 2020, followed by a decline to almost zero by 2080 and global population will reach its peak at slightly over 9 billion by the middle of the 21st century, with high global economic growth. The use of oil is expected to decline, while fossil- and biofuel use is projected to increase. No change is expected in decline in forest vegetation cover (IPCC 2013).

In the worst-case scenario (RCP8.5), greenhouse gas emissions will increase from around 8 Gt in 2000 and stabilize at just below 30 Gt of carbon by 2100. The assumption is that atmospheric concentrations of CO_2 will accelerate, reaching 950 ppm by 2100. Growth of population will be high, reaching 12 billion by the turn of the century. Economic growth is similar as in RCP6 but assumes that much lower income and per capita growth in developing countries. Under this scenario, energy consumption will be highly intensive. The total energy consumption will grow continuously and exceed over 3 times the current levels. The use of oil will grow rapidly up to 2070, after which it will drop at an even faster rate. Much of the increase in energy consumption will be due to coal use. The current land use trends will continue. With a decrease in forest area, crop and grass areas will increase (IPCC 2014c; van Vuuren 2011; Wayne 2013). According to the IPCC's high emissions scenario (IPCC 2014), the average global temperature could rise by 2.6–4.8°C by 2100.

The measured values for each anatomical variable were plotted as a function of the past rainfall data. As a second step, a least-squares regression line (calculated using Origin™) was fitted to the data. This was checked for linearity or the absence of non-linearity in the pattern of the data. Once a good fitting model was determined, the equation of the regression function for each property and species was determined, including the regression coefficient R. A well-fitting regression model was considered one in which a large proportion of the variance in wood anatomy values could be explained by the model. The regression functions were of the form $\mathbf{Y = a + b \cdot X +} e$, where a is the intercept, b is the slope and *e* is the residual error. P-values and confidence intervals for the estimate of the regression coefficients were used to determine significant variable contributions.

Chapter 4 Growth response of three Miombo tree species to climatic effects

4.1 Tree variables

For each species, the results of the data analysis indicating mean values (with standard deviation) for sample trees for each of the species for each site are shown in Table 4.1.

Table 4.1: Size, height and age distribution of the sampled trees

Site	Tree species	n (trees)	DBH (cm)	Height	Tree age (years)
			Mean ± SD	Mean ± SD	Mean ± SD
Livingstone	*B. spciformis*	20	32.0 ± 0.06	11.7 ± 2.2	34 ± 08
Lusaka		30	31.7 ± 0.07	12.7 ± 2.4	52 ± 12
Choma		16	38.0 ± 0.09	12.6 ± 2.2	74 ± 21
Kitwe		37	29.8 ± 0.06	15.2 ± 1.8	40 ± 10
Mwinilunga		30	35.0 ± 0.11	17.0 ± 2.7	46 ± 07
Livingstone	*Burkea africana*	15	30.0 ± 0.04	10.2 ± 0.8	27 ± 07
Choma		20	26.0 ± 0.05	7.9 ± 1.5	40 ± 10
Mwinilunga		21	24.2 ± 0.05	14.7 ± 2.1	40 ± 08
Kitwe	*Isoberlinia angolensis*	20	28.6 ± 0.04	12.9 ± 1.8	37 ±05
Mufulira		16	25.4 ± 0.01	12.2 ± 1.5	43 ± 15
Lusaka		20	34.0 ± 0.09	10.2 ± 2.2	44 ± 11

In *Brachystegia spiciformis* (p=0.02), *Burkea africana* (p=<0.001) and *Isoberlinia angolensis* (p=0.003), ANOVA revealed that site had a significant effect on mean tree diameter. In *Brachystegia spiciformis*, the paired t-Test (p=0.03) revealed that the mean DBH in Zone II (DMI: 21) differed significantly from that in Zone III (DMI: 33), but differences in mean DBH between the other sites were not significant (p>0.05). For *Burkea africana,* differences in DBH could also be explained by site. Post hoc tests revealed that significant differences in the means of stem diameter existed between the wettest site (Zone III) and the driest site in Zone I (p=0.004) and between the site in Zone III and the site in Zone II (p=0.007). In *Isoberlinia angolensis,* DBH means between the site in Zone I and the two in Zone III (Kitwe, p=0.007; Mufulira, p=0.02) differed significantly, but the difference in the means of DBH between trees from the sites in Zone III was not significant (p>0.05). The variations in DBH, total height and tree age for the different sampled trees for each species on different sites are graphically shown in Figures 4.1 to 4.3, respectively.

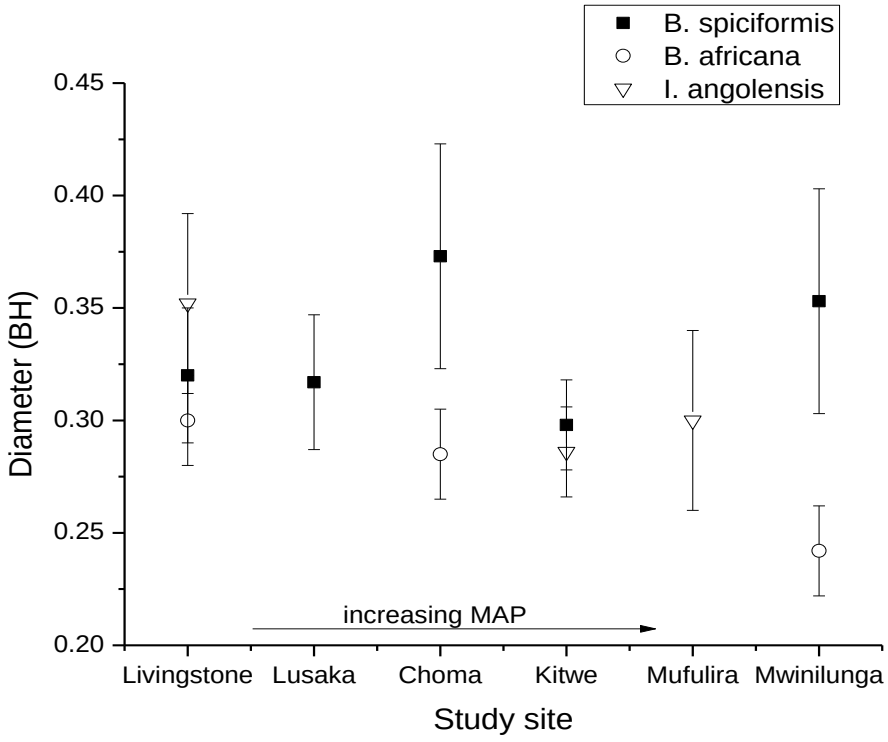

Figure 4.1: Variation in diameter (at breast height) of the three species for different sites

Sample variance for DBH in *B. spiciformis* was highest on the wet site in Zone III (0.0127) and the lowest on the dry site in Zone I (0.0038) and for *Burkea africana,* the sample variance was highest in Zone II (0.0034) and lowest in Zone I (0.0017), whereas for *Isoberlinia angolensis*, the variance was highest (0.001) in the dry Zone I (Lusaka) and lowest (0.0002) in the wet Zone III.

Data for total tree height measurements were analysed to compare means by site. Results for the variation of mean tree height within and between sites for all the species are graphically illustrated in Figure 4.2.

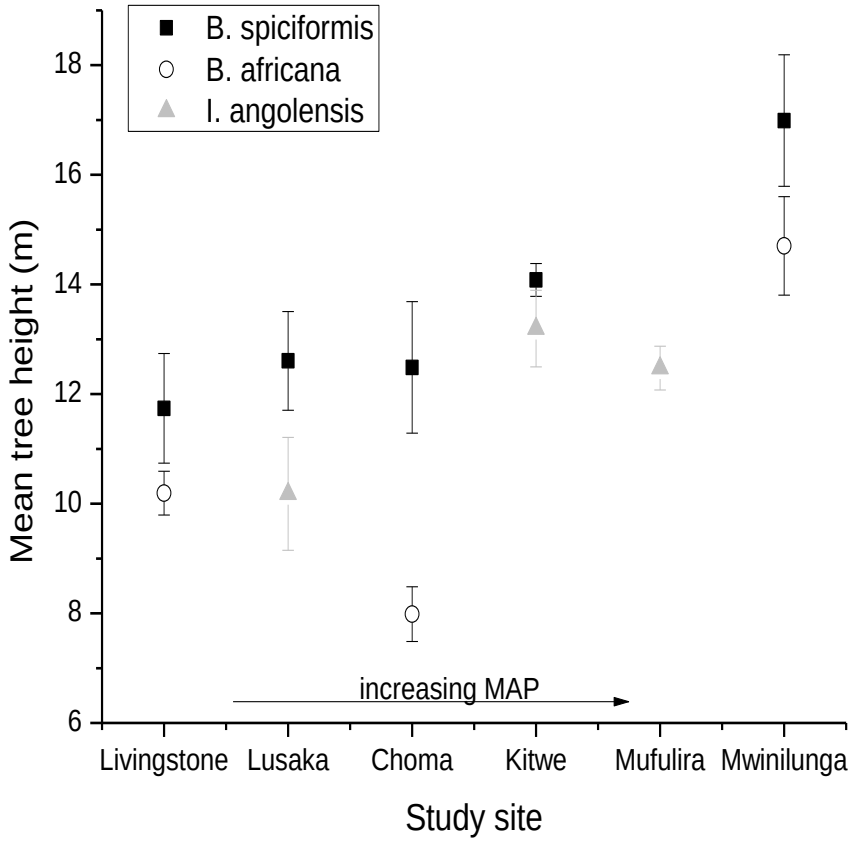

Figure 4.2: Variation of mean tree height by species and site

In *Brachystegia spiciformis* and *Burkea africana*, the p-value corresponding to the F-statistic of ANOVA was found to be lower than 0.05, which suggests that site conditions had an influence on mean tree height. In *Brachystegia spiciformis*, the Tukey HSD test revealed that mean tree height for the sites in Zone I differed significantly from that of sites in Zone III (Livingstone / Kitwe and Mwinilunga, p=<0.001; Lusaka / Kitwe, p=0.02 and Lusaka / Mwinilunga, p=<0.001). The mean height (p<0.02) for trees in Zone II differed significantly from that of the trees in Zone III. Results of a pairwise comparison of mean tree height (p=0.55) for sites in Zone I and the site in Zone II showed that the difference is not significant. In *Burkea africana*, significant differences (p=<0.001) were observed in the means of tree height between all the sites. Most of the *Burkea africana* trees in Choma appear to have been previously growing as suppressed trees, which remained in open space after removal of dominant species. In *Isoberlinia angolensis*, the difference in mean tree height between the two sites in Zone III was found to be statistically not significant (p=0.39). The mean height of *Isoberlinia angolensis* trees from Zone I (DMI, 20) was found to be significantly different (p=0.0001) from that of trees from Zone III (DMI, 33).

Tree height variance in *Brachystegia spiciformis* was found to be higher at the wet site in Mwinilunga and lowest in Kitwe. Variance in *Burkea africana* was higher in Zone III (DMI 34) and lower among trees in Zone I (DMI, 15)). In *Isoberlinia angolensis*, height variance was higher on the wet sites.

The variation of mean tree age for each species and site is graphically shown in Figure 4.3.

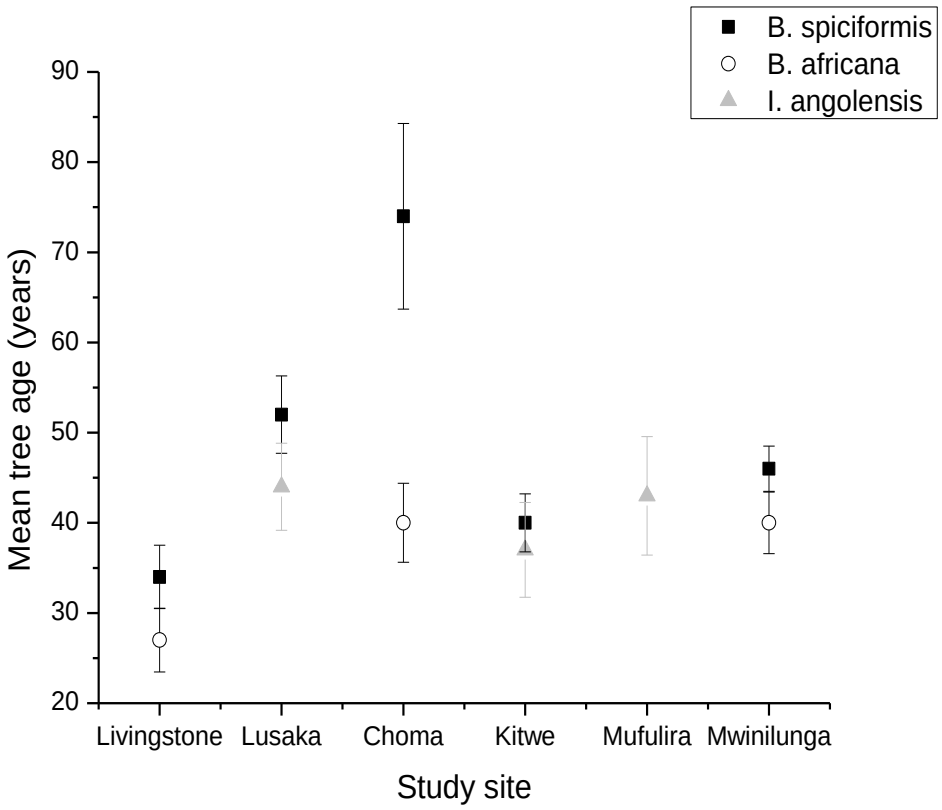

Figure 4.3: Mean tree age by species by site

In *Brachystegia spiciformis*, ANOVA indicated that there is statistically significant difference in mean tree age between sites ($p<0.02$. Tukey HSD test results for comparison of mean age for the trees from the two wet sites revealed no significant effect of site ($p=0.55$). Mean tree age ranged from 35 (Zone I; DMI: 20) to 74 years (Zone II; DMI: 21). The highest sample variance could be seen at Choma and the lowest in Mwinilunga.

In *Burkea africana* ($p=0.08$) and in *Isoberlinia angolensis* ($p=0.15$), results from ANOVA showed that the site had no effect on mean tree age. In *Burkea africana,* the oldest trees (mean age 40 years) were found in Zone II (DMI: 21) and III (DMI: 34) and the youngest (mean age 27 years) in Zone I (DMI: 15). The mean sample variance of tree age in *Burkea africana* was the highest in Choma and

lowest in Livingstone. In *Isoberlinia angolensis*, the mean tree age ranged from 37 years (Zone III, DMI: 33) to 44 years (Zone I, DMI: 20) and the sample variance was similar across sites.

Observed differences in tree variables (height, diameter, crown size) can be explained by differences in site conditions and by how competitive the species/tree is (Holdo 2006; Pretzsch *et al.* 2015). Genotype (Boyden *et al.* 2008; Zytynska *et al.* 2011), intrinsic tree characteristics (Coomes and Allen 2007), its functional traits (Chaturvedi *et al.* 2011), extrinsic variables like competition (Stoll and Newbery 2005), differences in light quality and quantity (Dong *et al.* 2012; Rüger *et al.* 2011), levels of soil nutrients (Baker *et al.* 2003; Baribault *et al.* 2012; Santiago *et al.* 2012) and natural or anthropogenic site disturbances (Bowman *et al.* 2013) are some of the major factors affecting tree growth. In this study, tree size, age and competitive ability within stands accounted for some of the differences in tree variables within and between stands. The results of the study suggest that there was a significant effect of site conditions on some of the tree variables. In a tree, the combination of temperature, water availability, variations in growth regulators and quantity of nutrients, determines the timing of growth ignition and cessation, the rate of cell division and the amount of cell expansion. Research has shown that through the variation in resource allocation, tree physiology and height can be linked to climate (Niklas 2007).

On the study sites, mean tree height increased from the low rainfall zone to the higher rainfall areas. At the dry end of the rainfall gradient, trees of all sampled species were found to be larger in diameter but shorter. Maximum tree height is determined by available resources, stresses encountered and competition for light (Givnish *et al.* 2014; Koch *et al.* 2004). Givnish *et al.* (2014) indicated that with increase in relative moisture supply, the maximum tree height should increase. Apart from water availability, difference in stand density between forest reserves in the dry and wet Miombo also result in differences in tree growth. Canopy stature of a species has been found to correlate well with its growth rate (Chi *et al.* 2015). Levels of crown illumination determine difference in growth between large-statured species and small-statured ones (Baker *et al.* 2003; Niinemets 2010). In the wet Miombo, stand density is typically high and trees must compete not just for growing space but also for light. This results in taller trees with smaller crown (except in areas where anthropogenic activities have changed the stand structure). In large parts of Zone I, trees often grow in open spaces and form wide crowns and grow to smaller heights. Becker *et al.* (2000) and Niklas (2007) explain that in large trees, height is constrained by a combination of mechanical and hydraulic requirements, each of which plays an important, but different role. As shown in Figure 4.5, on sites were all the three species were present, a higher growth rate in *Brachystegia spiciformis* enabled the species to dominate the upper canopy.

The growth of a tree within a stand is influenced by an interaction of biotic and abiotic factors (Coomes and Allen 2007; Robin-abbott and Pardo 2017; Stephenson *et al.* 2014). Compared to soil

and site disturbances, however, climate has been found to be a stronger determinant of growth (Feeley *et al.* 2007; Toledo *et al.* 2011). Analysis of data from the three zones revealed that differences in mean tree diameter could not only be attributed to site conditions. Since only large diameter trees were targeted, it was, however, not possible to have the structure of the woodlands from where sampling was done accurately described using diameter distribution. In a study on the Miombo woodlands of Tanzania, Isango (2007) found an inverse J-shaped diameter distribution.

Additionally, on all the sites and in all species, though differences were observed in mean tree age, these could not be attributed to climate-related variables but can rather be attributed to human activities in the forest reserves. The site in Zone II had the oldest trees because the stand from where sampling was done has been reserved and protected as a research stand. On the other sites, one finds succession and not primary forests.

4.2 Mean sensitivity

Analysis of the growth data shows that it was higher in trees growing in stressful locations and was reduced in trees growing under optimal conditions. For *Brachystegia spiciformis*, the lowest sensitivity (0.36) was found on the wettest site (Zone III, MAP = 1332 mm, DMI 34), while the highest sensitivity (0.50) was apparent on the driest site (Zone I, MAP = 697 mm, DMI 15). Similarly, for *Burkea africana,* a higher sensitivity was found on drier sites, while wetter sites showed a rather complacent growth pattern. The highest sensitivity (0.44) occurred on a dry site and the lowest (0.32) was found on the wettest site in Mwinilunga. *Isoberlinia angolensis* showed similar growth response patterns: the highest sensitivity (0.46) was found among trees growing on a dry site (Zone I, MAP = 802 mm, DMI 21) and the lowest (0.33) was found on a wet site (Zone III, MAP = 1293 mm; DMI 33). In all the species, the mean sensitivity had a strong negative correlation (R = -0.95) with MAP. Regression analysis further showed that the predictor variables for each of the species are significant (*Brachystegia spiciformis* R^2 = 0.94, p=0.002*; Burkea africana* R^2 = 0.98, p=0.04; *Isoberlinia angolensis* R^2 = 0.99, p=0.002). Pearson's correlation test showed that there is a strong association between rainfall and sensitivity. Regression coefficients in *Burkea africana* and *Isoberlinia angolensis* are higher because of the fewer study sites. The mean sensitivity values for each species and site are presented in Table 4.2.

Table 4.2: Ring width response to MAP and DMI

Species	Site	MAP (mm)	DMI	Sample variance	Mean sensitivity
B.spiciformis	Livingstone	697	15	0.016	0.50
Brachystegia spiciformis	Lusaka	802	20	0.005	0.47
Brachystegia spiciformis	Choma	806	21	0.003	0.44
B.spiciformis	Kitwe	1293	33	0.002	0.37
Brachystegia spiciformis	Mwinilunga	1332	35	0.005	0.36
Burkea africana	Livingstone	697	15	0.004	0.44
Burkea africana	Choma	802	21	0.013	0.41
Burkea africana	Mwinilunga	1332	35	0.012	0.32
I.angolensis	Lusaka	802	21	0.022	0.46
Isoberlinia angolensis	Kitwe	1293	33	0.010	0.34
Isoberlinia angolensis	Mufulira	1292	33	0.005	0.33

The relationship of mean sensitivity and precipitation is illustrated in Figure 4.4 and tabulated in Table 4.3.

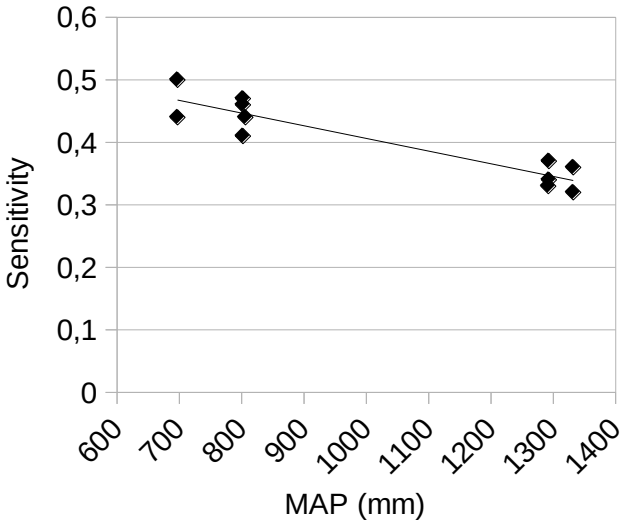

Figure 4.4: Linear regression of the relationship of sensitivity and mean annual precipitation of all three studied species

Table 4.3: Regression statistics of the influence of MAP and tree species on the sensitivity of tree-ring width. *Burkea africana* serves as the reference species in the regression.

Variable	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.584	0.018	32.90	< 0.001***
MAP (mm)	0.000	0.000	-12.37	< 0.001***
Brachystegia spiciformis	0.047	0.011	4.42	0.00308**
Isoberlinia angolensis	0.025	0.012	2.03	0.082
F-statistic: p-value: 0.0002			R = 0.97	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Ring width was expected to correlate with climate data, especially with DMI and MAP, since a plant responds to change in environment through gradual alteration of its growth rate, which allows the study of climatic variation through the ring width of the trees. In their studies on Miombo species Fichtler *et al. (2004)* and Trouet *et al.* (2006, 2010, 2012) also reported significant correlation of ring width and climate.

Results from this study indicate that the sampled tree species are sensitive to and respond to changes in their environment, and the growth response to water availability was positive and explained more than 90% of the inter-annual variation in secondary growth across the climate zones. As expected, a low degree of growth variation ('complacent' growth) from year-to-year was found on sites with higher water availability. As explained by Hughes *et al.* (2009), trees growing on sites where climatic factors are most frequently limiting, are the most likely to be responsive to climatic changes. Successful cross-dating between trees growing in the same stand indicates that growth of those trees was influenced by similar external factors (Babst *et al.* 2013; Carrer and Urbinati 2006; Worbes 1995). For dendrochronological studies, however, complacent growth poses a challenge. In trees with a low degree of year-to-year growth variation many of the rings appeared similar for many consecutive years and cross-dating tends to be difficult (Ngoma *et al.* 2017). In the more sensitive trees, the presence of micro rings close to wider ones has also been found to cause cross-dating problems (Speer 2010). In *Isoberlinia angolensis,* ring boundaries became indistinct in some sections of the radius, resulting in cores, in which cross-dating could not be performed successfully.

For all species, the variance in ring width decreased with increasing MAP, with the greatest variance being found on the dry sites where rainfall, the main growth limiting factor, varies highly from year-to-year. On the sites in Zone I, inter-annual variability of rainfall is typically very high, resulting in clear growth variations, while on sites in Zone III, growth was more stable. The higher sensitivity on the drier sites is indicative of how much tree growth on these sites is limited by rainfall.

4.3 Growth response to water availability and temperature

The correlation between ring width and water availability (DMI) was determined for each site and species. To determine the individual impact of temperature and precipitation (MAT and MAP), these correlations were additionally determined. The correlation coefficients for each species are listed in Table 4.4.

Table 4.4: Ring width correlation with DMI, MAP and MAT

Species	Site	RW/DMI R	RW/MAP R	RW/MAT R
B. spiciformis	Livingstone	0.42	0.42	0.10
B. spiciformis	Lusaka	0.50	0.50	0.14
B. spiciformis	Choma	0.45	0.45	0.00
B. spiciformis	Kitwe	0.42	0.42	0.17
B. spiciformis	Mwinilunga	0.47	0.42	0.14
B. africana	Livingstone	0.46	0.46	0.14
B. africana	Choma	0.51	0.51	0.00
B. africana	Mwinilunga	0.42	0.42	0.14
I. angolensis	Lusaka	0.44	0.36	0.00
I. angolensis	Kitwe	0.20	0.37	0.14
I. angolensis	Mufulira	0.40	0.40	0.14

From Table 4.4, a weak but positive association of ring width with water availability can be seen, which shows that variation in ring width can partly be attributed to variation in water availability during periods of cambial activity.

For tree growth response to water availability, ANOVA results indicate that significant differences ($p=0.04$) in ring width exist among the sites for *Brachystegia spiciformis*. Pairwise comparison of means using the Tukey HSD test showed that the difference in RW means between trees from the two sites in Zone III was found to be not significant ($p=0.63$). For *Burkea africana,* and *Isoberlinia angolensis* the post hoc tests revealed that the difference in RW means between sites in Zones I, II, and III was statistically significant ($p<0.05$). In *I. angolensis* the mean of RW for the dry site (Lusaka) differed significantly ($p=0.04$) from that for the two wet sites (Kitwe and Mufulira), but the mean RW between the two wet sites ($p=0.07$) was not significantly different statistically.

A seven-year period (2000-2007) saw a marked increase in the intensity and frequency of extreme climate events (i.e. droughts and floods) during the core of the rainy season due to El Niño (McSweeney *et al.* 2008; Bwalya 2010). Scenarios based on global climate models strongly suggest that MAP/MAT will change across Zambia (McSweeney *et al.* 2008). The projected changes show an increase of MAT around 1.2 – 3.4˚C by 2060, with a substantial increase in the frequency of hot

days and nights. MAP is predicted to decrease by 15 - 20% in intra-annual rainfall averages throughout the year.

By the 2060s, Zambia can expect a MAP of 800 - 900 mm (currently 1032 mm) and a rise in MAT to ca. 23 - 25°C from the current 21°C (World Bank 2018).

The analysis of ring data revealed that tree growth correlated well with rainfall at each site. The correlation of RW with water availability was found to be weak, but positive. The low correlation coefficients can be explained by the fact that the environment in which a tree grows is not defined by just the level of wetness, but by several other confounding external factors (Coder 1999). On the selected study sites, the main growth limiting factor was water availability and not temperature. When growth is not limited by other factors, tree growth responds positively to an increased water availability. Research (e.g. Berner *et al.* 2017) has shown that net primary productivity in trees increases with increase in level of wetness. Through its direct effect on turgor, or indirect effect by limiting carbon gain, water stress limits tree growth (Teskey and Hinckley 1986). Trees growing in Zones I and II are often subjected to periods of water stress due to frequent droughts.

The effect of temperature on tree growth was slightly negative for all species. The correlation coefficients were very small, which means that tree growth is almost non-responsive to temperature. The effect of temperature is mitigated by precipitation during periods of tree growth. As reported by Yang *et al.* (2006), a significant rise in temperature negatively affects growth due to the resulting increase in evapotranspiration, whereas precipitation positively affects tree and forest growth. Plant growth negatively correlates with temperature (Fitter and Hay 2012; Levesque *et al.* 2017) resulting in increased loss of assimilated carbon (Fichtler *et al.* 2004). It has been suggested by Bowman *et al.* (2014) that the interpretation of temperature responses is complicated, due to the indirect effects it has, via evaporation, on water availability, as well as direct metabolic effects. Although MAT is higher on the wet sites, higher MAP seems to moderate the effects of increased evapotranspiration. Higher moisture levels ensure that there is a good photosynthetic and respiration balance in the tree. This balance, according to Coder (1999), is the main biological feature influencing ring width. Hasanuzzaman *et al.* (2013) reported that temperature increase in plants up to the optimum level increases physiological processes, i.e. growth, photosynthesis, respiration and enzyme activity. Beyond this optimum level, a decline in these parameters can be observed.

4.4 Conclusions

This study focused on whether the growth response of each of the three sampled species to climatic variations across the zones is the same, bearing in mind the differences in growing conditions.

Results showed that the interaction between site conditions and most of the tree attributes is significant. Tree variables differ depending on an interaction of biotic and abiotic factors, which include soil characteristics, topography, climate, competitive interactions and anthropogenic deposition.

All three species show that inter-annual ring width variations were as a result of fluctuations in environmental conditions at each site, with water availability having a much larger effect than temperature, especially on the drier sites. On the sites in Zone I, all species exhibited greater variation in growth from year-to-year. All three species showed different sensitivity to climatic variations, depending on the water availability, which indicates that growth and maybe dominance in population will shift, if climatic conditions are getting dryer. *Brachystegia spiciformis* and *Burkea africana* seem to be more tolerant than *Isoberlinia angolensis* and might benefit from the lower performance of drought sensitive species. However, for more conclusive results, a larger data set especially for *Isoberlinia angolensis,* on more sites, is needed.

Temperature had significantly less effect on ring width than precipitation and DMI showed comparable results to MAP. This means that water is the main limiting factor and should be considered most when determining the vulnerability of Miombo tree species to climate change. We expect a static correlation between water availability and tree growth.

Knowledge of climate trends coupled with tree-ring research may help to predict the effect the expected change in climate will have on tree growth and on wood quality. Significant variation in growing conditions due to change in climate could result in change in quality of wood from these and other Miombo tree species. The more variation in properties wood has, the less suitable the wood might be, especially for applications, in which strength is the key consideration. Variation in properties will make it difficult for the timber from these species to fulfil explicit or implicit design strength requirements. Knowledge of how trees respond to factors affecting their growth is important for predicting potential changes that may occur under changing environmental conditions.

Chapter 5 The expected effects of climate on selected anatomical properties of three Miombo tree species

5.1 Fibre properties

The relationships between the mean value of each anatomical property and the level of wetness is explained by the model $y=a*x^b$, where y is the anatomical property being studied, a and b are coefficients, and x refers to the aridity index.

5.1.1 Cell wall thickness

The variations in mean cell wall thickness (CWT) and 95% confidence intervals for *Brachystegia spiciformis*, determined from CT analysis for dry and wet years, is graphically presented in Figure 5.1.

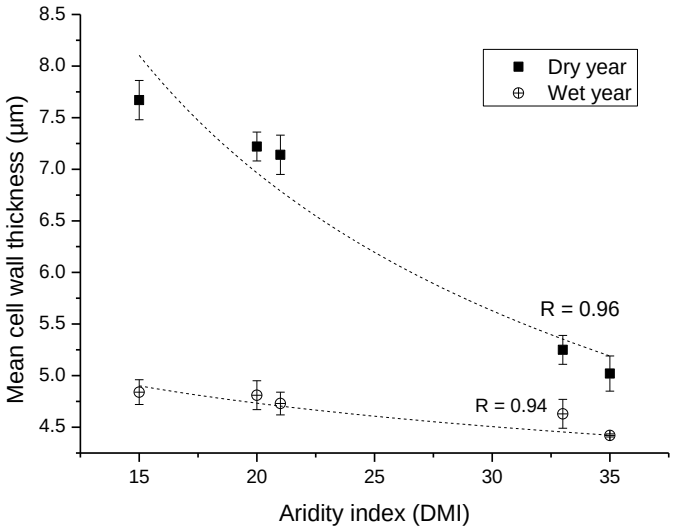

Figure 5.1: Mean CWT and 95% confidence bands of *Brachystegia spiciformis* plotted against DMI

ANOVA results showed statistically significant differences in the mean CWT among sites for both dry (p=<0.001) and wet years (p=0.02) in *Brachystegia spiciformis*. As shown in Figure 5.1, a change in water availability during periods of tree growth and wood production led to differences in cell wall thickness, with mean CWT generally decreasing with an increase in water availability. A summary of the t-Test results from the pair-wise comparison of CWT in the dry year for all the species is presented in Table 5.1.

Table 5.1: Bonferroni test results for differences in CWT between sites

Sites	*B. spiciformis*	*B. africana*	*I. angolensis*

	t Value	Sig	t Value	Sig	t Value	Sig
Lusaka v. Livingstone	-1.834	0				
Choma v. Livingstone	-2.259	0	-6.123	1		
Choma v. Lusaka	-0.320	0				
Kitwe v. Livingstone	-10.298	1				
Kitwe v. Lusaka	-7.985	1			-5.681	1
Kitwe v. Choma	-8.039	1				
Mwinilunga v. Livingstone	-10.773	1	-13.839	1		
Mwinilunga v. Lusaka	-8.559	1				
Mwinilunga v. Choma	-8.619	1	-8.697	1		
Mwinilunga v. Kitwe	-0.954	0				
Mufulira v. Lusaka					-5.991	1
Mufulira v. Kitwe					-1.725	0

Sig = 1 indicates that the means difference between the two sites is significant at a 0.05 level, while Sig = 0 indicates that the means difference is not significant at a 0.05 level.

In *Brachystegia spiciformis,* the difference between sites in the drier zone and those in the higher rainfall zones was statistically significant (p=<0.001), but the difference between the two dry sites in Zone I (p=0.07) and between the two wet sites in Zone III (p=0.89) was not significant.

The fit functions from the allometric model ($y=a*x^b$) explaining the change in mean CWT with change in level of wetness for each of the species are presented in Table 5.2

Table 5.2: Response of mean CWT to extreme events

	Dry period			**Wet period**		
Species	**a**	**b**	**R**	**a**	**b**	**R**
Brachystegia spiciformis	33.66	-0.53	0.96	6.81	-0.12	0.95
Burkea africana	36.10	-0.58	0.99	4.38	-0.02	0.97
Isoberlinia angolensis	165.17	-1.01	0.99	45.10	-0.71	0.81

At all sites, further comparison of mean values of the cell walls formed in the dry and wet years showed statistically significant differences (p<0.02). The differences were found to be larger on the drier sites, than on the wet sites. Across the sites, thicker cell walls were formed in the dry year. The thickest cell walls, with a mean of 7.67 µm, were formed during a dry year on the driest site (Livingstone) and the thinnest cell walls, with a mean of 5.02 µm, were formed in a wet year on the wettest site (Mwinilunga). For dry and wet year CWT in *Brachystegia spiciformis,* results for Levene's test of equal variance indicate that at the 0.05 level, the sample variances (p>0.05) are not significantly different.

In the wet year, ANOVA showed that the means difference between sites was not significant in *Brachystegia spiciformis* and in *Burkea africana* and the wet sites was significant (p<0.05).

The CWT variation in *Burkea africana* and *Isoberlinia angolensis* is represented in Figure 5.2a and b, respectively.

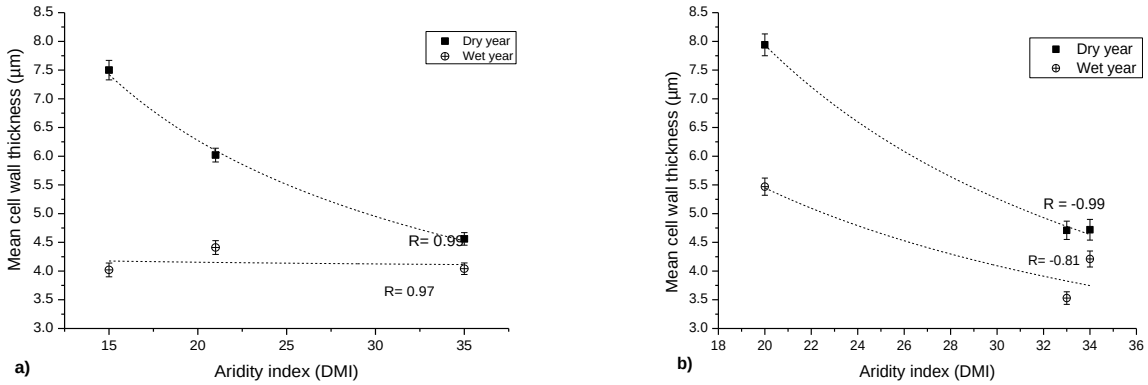

Figure 5.2: Mean CWT as a function of DMI in a) *Burkea africana* and b) *Isoberlinia angolensis*

For *Burkea africana,* in both the dry year (p<0.001) and the wet year (p=0.02), statistically significant differences between sites were found. In the wet year, t-Test results (p=0.02) revealed statistically significant differences between the means of the dry and the mildly-wet sites and between the mildly-wet site and the wet site. The difference between the dry site and wet site was, however, not significant (p=0.88).

Mean cell wall thickness in *Burkea africana* ranged from 4.04 µm on the wettest site (Mwinilunga) to 7.5 µm at the driest site (Livingstone). At all sites the difference between dry and wet year CWT was statistically significant (p<0.01). The exception was at the wettest site (p=0.75), where the difference was found to be statistically not significant. For dry year CWT, results for test of equal variance (p=0.03) indicate that the sample variances are significantly different, while they were not significantly different for the wet year (p=0.17).

In *Isoberlinia angolensis* the CWT differed significantly (p<0.01) between sites for both the dry and wet year. CWT was significantly different between the dry site (Lusaka) and the two wet sites (Kitwe and Mufulira) (p=0.001), however, no statistically significant difference (p>0.05) could be found between the two wet sites. At the 0.5 level, the sample variances in the dry year (p=0.02) and in the wet year (p=<0.001) were found to be significantly different.

In wet years, site interacted significantly (p<0.01) with CWT. The post hoc test revealed that the means difference for the drier site (Lusaka) and the two wet sites (Kitwe and Mufulira) was statistically significant (p=0.001). The difference in CWT means at the two wet sites was also

statistically significant (p=0.006). This was a surprising finding, since in the dry year, the two sites produced similar CWT means. Another observation made was that across all species on the dry study sites, the variance was larger during the dry years compared to that for the wet years.

A large difference can be seen between dry and wet year CWT. Cell wall thickness variation as a function of site was found to be large for dry years and minimal for the wet years. In all species (*Brachystegia spiciformis:* R = -0.96, *Burkea africana:* R = -0.99, *Isoberlinia angolensis:* R = -0.99), CWT showed a strong negative correlation with DMI in the dry-year and the effect of limited water supply became more apparent on the already water stressed, dry sites. In the wet year (*Brachystegia spiciformis:* R = -0.94, *Burkea africana:* R = -0.97, *Isoberlinia angolensis:* R = -0.81), a large proportion of the change in mean CWT could be explained by level of wetness. From Table 5.2, *Isoberlinia angolensis* shows more sensitivity to changes in level of wetness compared to *Brachystegia spiciformis* and *Burkea Africana* which seem to be more resilient. The observed differences in mean CWT change across the sites is indicative of the vital role water availability plays during growth, and supports the findings of other studies (Eilmann *et al.* 2011; Eilmann and Rigling 2012; Kreuzwieser and Gessler 2010; Lundqvist *et al.* 2017; Wagner *et al.* 2012), all of which linked limited water resources to slower growth and thicker cell walls. CWT directly affects wood density and by extension the wood quality and fibre yield and quality.

5.1.2 Fibre diameter

The effects of water availability were also reflected in the different means of fibre diameter (FD) among sites and between the two extreme climate events. FD variation is illustrated in Figure 5.3 for *Brachystegia spiciformis* and in Figure 5.4a and b for *Burkea africana* and *Isoberlinia angolensis*, respectively.

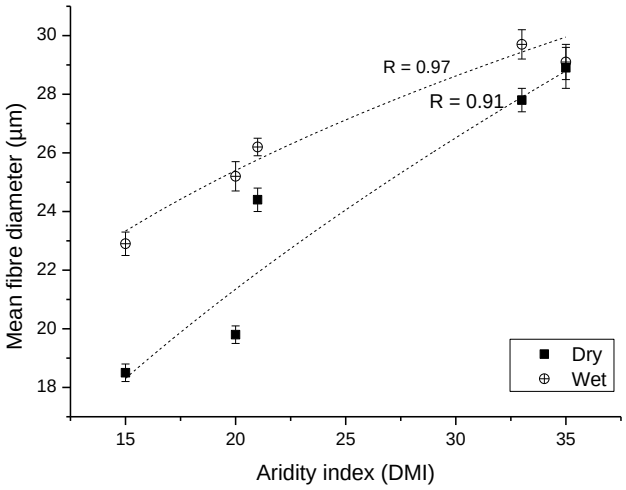

Figure 5.3: Mean FD as a function of DMI in *Brachystegia spiciformis*

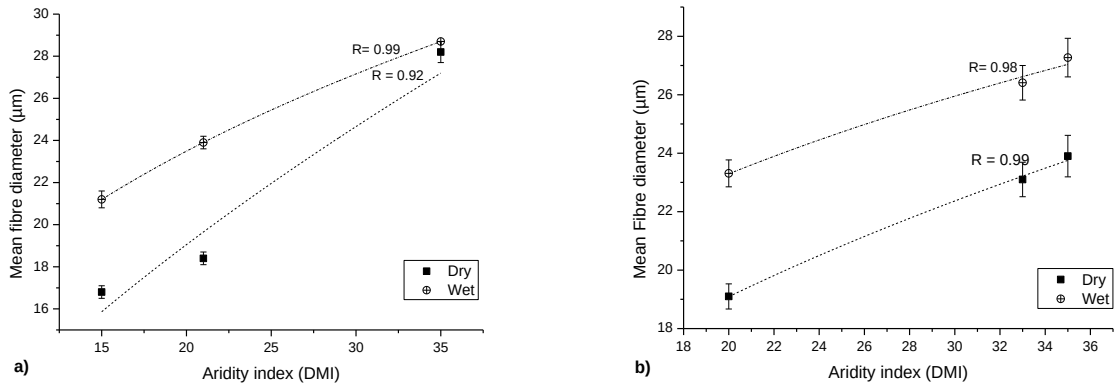

Figure 5.4: Mean FD as a function of DMI in a) *Burkea africana* and b) *Isoberlinia angolensis*

For differences in FD means, post hoc test results for each species are shown in Table 5.3

Table 5.3: Bonferroni test on differences in FD between sites

Sites	***B. spiciformis***		***B. africana***		***I. angolensis***	
	t Value	Sig	t Value	Sig	t Value	Sig
Lusaka v. Livingstone	2.21	0				
Choma v. Livingstone	9.58	1	2.98	1		
Choma v. Lusaka	7.22	1				
Kitwe v. Livingstone	15.25	1				
Kitwe v. Lusaka	12.76	1			4.78	1
Kitwe v. Choma	5.50	1				
Mwinilunga v. Livingstone	16.77	1	21.03	1		
Mwinilunga v. Lusaka	14.29	1				
Mwinilunga v. Choma	7.14	1	18.16	1		
Mwinilunga v. Kitwe	1.74	0				
Mufulira v. Lusaka					5.68	1
Mufulira v. Kitwe					0.90	0

In *Brachystegia spiciformis*, significant differences between the sites were found in both the dry year ($p<0.01$) and the wet year ($p=<0.001$). In the dry year the difference in FD between the two dry sites in Zone I ($p=0.18$) and between the two wet sites in Zone III ($p=0.41$) was found to be not significant. However, between each of the sites in Zone I and Zone III, the difference in FD was statistically significant ($p=0.001$). In the wet year, the difference in FD between Lusaka and Choma ($p=0.55$) and Kitwe and Mwinilunga ($p=0.89$) were statistically not significant. Pair-wise comparison of FD for the other sites revealed statistically significant differences ($p<0.01$).

Parameters from the allometric model explaining the observed effect of climate events on mean fibre diameter are presented in Table 5.4.

Table 5.4: Response of mean FD to extreme events

	Dry year			Wet year		
Species	a	b	R	a	b	R
Brachystegia spiciformis	4.31	0.53	0.91	10.51	0.29	0.97
Burkea africana	2.83	0.64	0.92	8.04	0.36	0.99
Isoberlinia angolensis	5.93	0.39	0.99	10.49	0.27	0.99

In *Brachystegia spiciformis* the smallest FD of 18.4µm was found on the driest site (Livingstone, DMI 15), formed in the dry year, while the largest FD of 29 µm, formed in the wet year, was found on the wettest site. The tests of equal variance indicated that sample variances for both dry year ($p<0.001$) and wet year ($p=0.03$) were significantly different.

For *Burkea africana*, the p-value in both the dry and wet year is lower than 0.01, which suggests that one or more sites differed significantly in FD. The t-Test revealed that the difference in FD between the dry and the mildly-wet sites ($p=0.01$), between the dry site and the wet site ($p<0.01$) and between the mildly-wet site and the wet site ($p<0.01$) were highly significant.

In the wet year, t-Test results ($p<0.001$) show significant differences in FD between all sites. Comparison of the dry and wet year showed statistically significant differences in FD at the dry and mildly-wet sites ($p=<0.001$), but no statistically significant difference ($p=0.46$) at the wettest site. The mean FD ranged from 16.8 µm in the dry year at the dry site (Livingstone, DMI 15) to 28.7 µm at the wet site in both years (Mwinilunga, DMI 35). For the dry year, the FD variances in *Burkea africana* are significantly different ($p=0.02$), while in the wet year ($p=0.90$), no statistically significant difference in sample variances was found.

In *Isoberlinia angolensis*, site was found to have a statistically significant effect on the FD for both dry ($p=0.001$) and wet years ($p=0.02$). In the dry year, the FD difference between the two wet sites (Mufulira and Kitwe) was not statistically significant ($p=0.62$). However, t-Test results ($p=0.001$) showed a statistically significant FD difference between dry and wet sites in Zone I and III.

In the wet year, the t-Test revealed statistically significant differences in FD between the dry site and the two wet sites, but between the two wet sites, the difference was not significant ($p=0.06$). Pairwise comparison of dry and wet year FD shows that water availability has a significant influence on FD at all sites ($p<0.01$). Mean FD in *Isoberlinia angolensis* ranged from 19.1 µm in the dry year at the dry site (Lusaka, DMI 20) to 27.3 µm in the wet year at the wet site (Kitwe, DMI 33). For the FD values of the dry year in *Isoberlinia angolensis,* the test of homogeneity showed that sample variances are

not significantly different (p=0.27), however, in the wet year the sample variances are significantly different (p=0.03).

FD correlated positively with DMI for all species, with R = 0.91 for *Brachystegia spiciformis*, R = 0.92 for *Burkea africana* and R = 0.99 for *Isoberlinia angolensis* in the dry year and *R* = 0.97 for *Brachystegia spiciformis, R* = 0.99 for *Burkea africana* and *R* = 0.98 for *Isoberlinia angolensis* in the wet year. As can be seen in Table 5.4, the biggest change in mean FD occurred on the dry site in both *Brachystegia spiciformis* and *Isoberlinia angolensis*. Because *Isoberlinia angolensis* occurs mostly in the wet Miombo, the change in mean FD during dry and wet years is not very different. Consistent with other studies (e.g. Crous *et al.* 2012; Eilmann *et al.* 2009; Fonti *et al.* 2013; Martínez-Cabrera *et al.* 2009), both FD and VD (section 1.3.2) were larger in wood formed during the wet year and on sites with higher DMI. The mean FD of wood formed during dry years was in all cases significantly smaller compared to that produced under wet conditions. However, the differences between dry and wet year became smaller with increased DMI. The biggest difference between the dry and wet year was seen on the dry sites (Zone I) and the smallest on the wet sites (Zone III). On sites in Zone III, trees produced wood with uniformly sized fibres, whether formed during a dry or wet year. In Zone I, the wood formed under water stressed conditions had fibres that were almost double the size of those formed during wet periods. Generally, wood formed in more arid zones is characterized by fibres with thicker cell walls and smaller lumen diameters. Like CWT, fibre diameter influences wood density, which is one of the major determinants of wood quality.

5.2 Vessel characteristics

5.2.1 Vessel count

The response of mean vessel frequency to the occurrence of extreme climate events is explained using allometric equation parameters shown in Table 5.5.

Table 5.5: Response of MVF to extreme events

	Dry year			**Wet year**		
Species	a	b	R	a	b	R
Brachystegia spiciformis	344.44	-0.84	0.93	63.45	-0.43	0.94
Burkea africana	185.36	-0.62	0.83	70.75	-0.47	0.99
Isoberlinia angolensis	6037.57	-1.86	0.99	2305.92	-1.65	0.98

The vessel frequency (VF) per unit area was found to decrease with an increase in level of wetness. In *Brachystegia spiciformis* (Figure 5.5), the difference in VF between the dry and wet year (p=0.03) was significant at all sites, except for Mwinilunga, the wettest site (p=0.92).

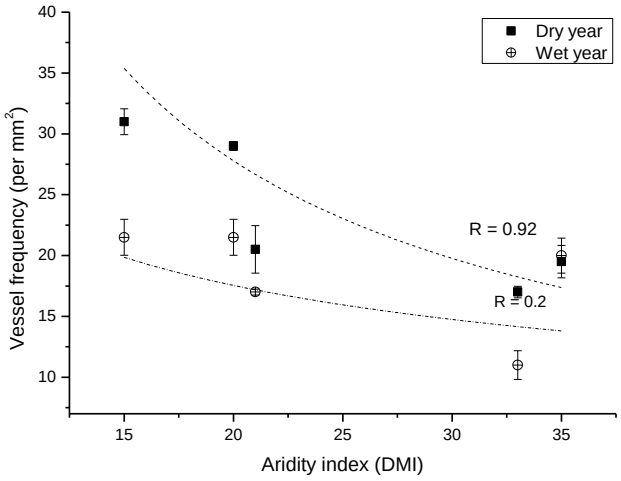

Figure 5.5: Mean VF as a function of DMI in *Brachystegia spiciformis*

The mean VF ranged from 17 in the wet Zone III to 31 in the dry Zone I in the dry year and from 11 in Zone III to 22 in Zone I in the wet year. For the dry ($p=0.003$) and wet year ($p=0.02$) results for Levene's test of equal variance indicate that the sample variances are significantly different in *Brachystegia spiciformis*. Since the variance homogeneity was affected and hence a one-way ANOVA was deemed inappropriate, a non-parametric test (the Kruskal-Wallis test) was used to determine whether the medians between groups of VF data were statistically different. Not only is this test less sensitive to outliers but it does not assume that the data being analysed is normally distributed in the data. The H (test) statistic showed statistically significant differences between the dry and years ($p<0.05$).

For *Burkea africana* (Figure 5.6a), statistically significant differences ($p=0.04$) in mean VF were found between sites, but between Zone II and Zone III the difference in mean VF was not significant ($p>0.05$). Comparison of mean VF for the wet and dry years indicates that the difference in VF between wet and dry years decreases visibly with increasing DMI. The mean VF ranged from 13 in the wet Zone to 22 in the dry Zone I in the wet year and from 20 in Zone III to 37 in Zone I in the dry year. For the dry year ($p<0.001$) and wet year ($p=0.01$) the test of equal variance indicates that the sample variances were significantly different.

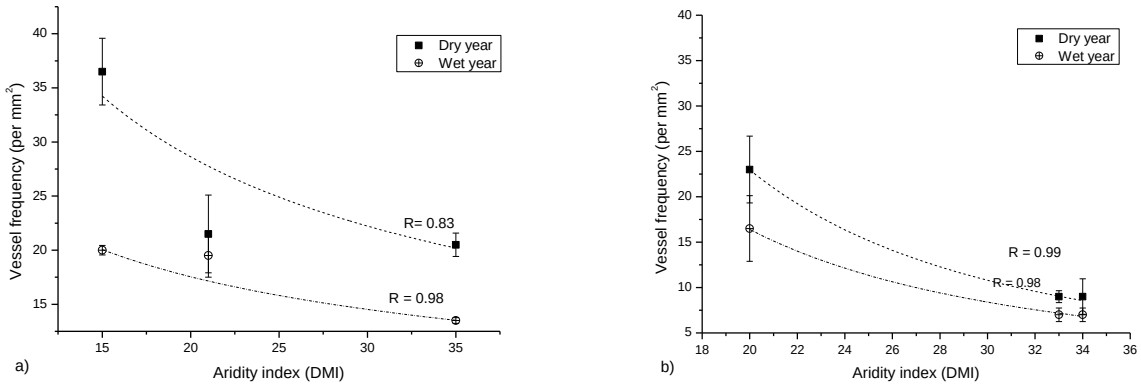

Figure 5.6: Mean VF as a function of DMI in a) *Burkea africana* and b) *Isoberlinia angolensis*

In *Isoberlinia angolensis* (Figure 5.6b), pairwise comparison of VF for the wet and dry years showed no statistically significant differences ($p>0.05$) between the dry and wet sites. However, in the trees growing in Kitwe (Zone III), a statistically significant difference ($p=0.04$) in VF between dry and wet year was found. The sample variances in the dry year ($p<0.001$) and in the wet year ($p=0.01$) were significantly different. Mean VF in *Isoberlinia angolensis* ranged from 7 in the wet year on the wet site to 23 in the dry year in on the dry site.

As can be seen in Figures 5.5 and 5.6, the wood formed during dry periods had more vessels compared to that formed during periods when water was less growth-limiting. These results are consistent with the findings of February *et al.* (1995), Drew and Pammenter (2006), Naidoo *et al.* (2007) and Drew *et al.* (2009), who all reported a reduction in vessel frequency with an increase in water availability. Drew and Pammenter (2006) explained that under higher stress conditions, rate of vessel production takes place at a significantly higher rate. On the drier sites, the wood forms more vessels, but with smaller diameters, compared to the small number of broad vessels found on wet sites and during wet years. The relationship between vessel count and water availability in the studied species is, however, not as clear as for CWT and FD and not necessarily linear.

Vessel coverage affects wood quality through its effect on wood density and a smaller vessel coverage translates into higher wood density.

5.2.2 Vessel diameter

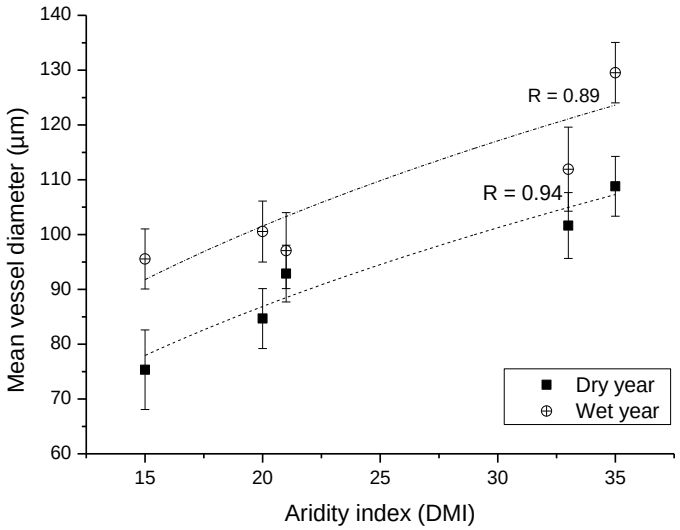

Figure 5.7: VD as a function of DMI in *Brachystegia spiciformis*

ANOVA of *Brachystegia spiciformis* (Figure 5.7) for the dry year ($p<0.001$) and in the wet year ($p=0.005$) showed that the VD means differed significantly between sites. In the dry year, the post-hoc test showed significantly different VD between Livingstone and Choma ($p=0.01$), Lusaka and Kitwe ($p=0.005$) and between Choma and the two wet sites (Kitwe, $p<0.001$ and Mwinilunga, $p=0.001$). The differences in VD between sites from the same zone were not statistically significant ($p>0.05$). Results of the test of equal variance indicate that there was insufficient information to draw conclusions.

Statistically significant differences were found in the wet year ($p=0.002$) between dry and wet sites, but the difference between sites in the same zone was insignificant ($p>0.05$). The VD in *Brachystegia spiciformis* ranged from 92.8 µm in the dry Zone I to 101.65 µm in the wet Zone III in the dry year and from 95 µm in Zone II to 129 µm in Zone III in the wet year.

In *Burkea africana* (Figure 5.8a) site had a significant influence ($p<0.001$) on VD in the dry year, but in the wet year differences between sites were insignificant ($p=0.63$). Post hoc test results showed significantly different VD in wood from trees in Zones I and II ($p<0.01$), while no significant difference ($p>0.05$) was found in the wood from Zone III trees. For the dry year ($p=0.0005$) and wet year ($p=0.01$) results for test of equal variance indicate that the sample variances are significantly different.

The mean VD ranged from 63 µm in the dry Zone I to 111 µm in the wet Zone III for the dry year and from104 µm to 111 µm for the wet year. Results of the Bonferroni HSD post-hoc test revealed that

the VD means between wood from trees found in Zone I and Zone II (p=0.002), Zone I and Zone III (p=0.001), and Zone II and Zone III (p=0.006) differed significantly.

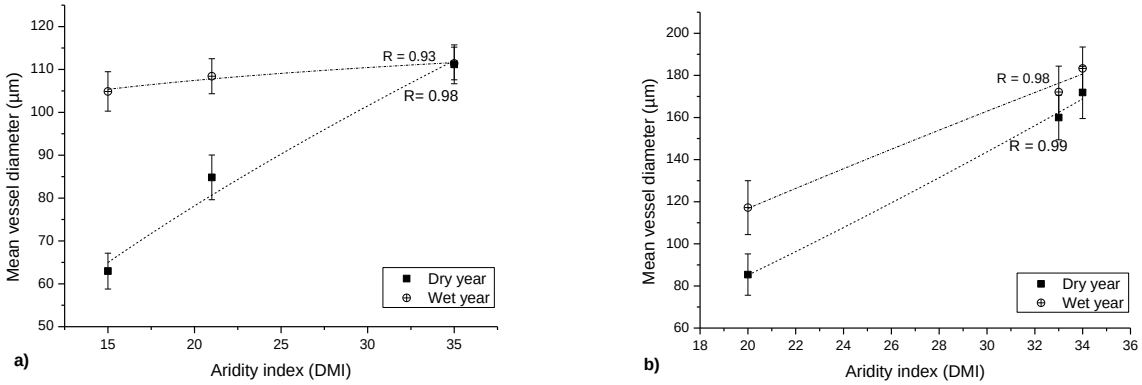

Figure 5.8*:* VD as function of DMI in a) *Burkea africana* and b) *Isoberlinia angolensis*

In *Isoberlinia angolensis* (Figure 5.8b) site significantly affects VD in both the dry ($p<0.01$) and wet year ($p=0.004$). The t-Test revealed statistically significant differences in VD between Zone I and the wet sites in Zone III ($p=0.001$), but the VD on the wet sites in Zone III was not significantly different. The sample variances were significantly different in both the dry- and wet years ($p<0.05$). The large difference led to the assumption that the analysed data was not normally distributed. For this reason, an alternative to one-way ANOVA, the Kruskal-Wallis test, was used to compare the medians. The mean VD ranged from 85.4 µm in the dry Zone I to 160 µm in the wet Zone III for the dry year, while for the wet year the VD ranged from 117 µm to 183 µm.

In wood from all species, the change in vessel diameter was significant across the sites. The general trend showed an increase in vessel diameter with increased water availability. Wood formed during dry years showed a larger number of smaller vessels, compared to the wider, but fewer vessels found in wood formed in wet years.

Comparison of the mean values of VD for the wet and dry year revealed that for all species and on most of the sites the difference between wet and dry years was significant ($p<0.05$).

Vessel diameter correlated positively with DMI in the dry years for *Burkea africana* (R = 0.98), *Isoberlinia angolensis* (R= 0.98) and *Brachystegia spiciformis* (R = 0.81). The correlation coefficients for the wet years were R = 0.97 for *Burkea africana,* R = 0.95 for *Brachystegia spiciformis* and R = 0.99 for *Isoberlinia angolensis*. There was an unexpected lower coefficient of determination in *Brachystegia spiciformis* at a site in Zone I, which could be due the interaction of growth in the area with factors other than climate.

Vessel size can cause problems in the end-processing of wood, especially in paper production, where large vessels are problematic (Chen *et al.* 2004). This would be especially so for wood sourced from the high rainfall areas of Zambia.

5.3 Conclusions

This study set out to test the effect of extreme events on wood anatomical properties of three selected Miombo tree species. Consistent with literature (e.g. February *et al.* 1995; Galle *et al.* 2010), a strong effect of water availability on wood anatomical properties was found for all species. The occurrence of extreme events during periods of cambial activity is reflected in the size and number of fibres and vessels. It can therefore be expected that the anatomical features of all three species under investigation will change with the expected climate change in future. Any significant change in cell size, i.e. cell wall thickness, fibre diameter, vessel diameter, ratio of earlywood to latewood and in chemical composition of the resulting wood will affect wood properties such as drying, hardness, stiffness, strength and machining, which are key to the use of solid wood and fibre products.

The results demonstrate that a decrease in water availability during growth results in smaller fibres, thicker cell walls, increased vessel frequency and smaller vessels. The projected increase in frequency and magnitude of droughts will thus potentially result in slower tree growth and in wood with a larger number of smaller-diameter vessels and narrower cells with thicker walls. This will lead to a higher wood density, which is desirable for most solid wood end-products at the cost of volume increment.

This study included three important tree species in the Miombo that were sampled in a reasonably large area of Zambia spread over climate zones. So, our findings can be interpreted with some confidence with regards to the reaction pattern and provide novel insights in the magnitude of wood anatomical changes in extreme years. However, there are certainly many more species that need to be investigated to develop a full picture of how Miombo trees respond to extreme climate events and data need to be collected from different areas as well to validate our findings. Thus, additional studies, involving a larger number of sites and samples, need to be carried out to develop reliable quantitative models of the reaction of wood properties to climatic influences that can be used in scenario analysis on impacts of climate change.

Chapter 6 Scenario modelling of the implications of climate change on wood anatomical properties of commercially important Miombo species

6.1 Introduction

The increase in greenhouse gases has led to global warming, which has caused a worldwide change in precipitation patterns, a rise in temperature and the increased occurrence of extreme weather events (IPCC 2007 2014a). This change in growth conditions of trees has implications on wood anatomy and wood quality. Though phylogenesis determines the qualitative structure of wood, climate influences wood's functional anatomy (Warwick *et al.* 2017) and the characteristics of the individual cells that make up wood are related to tree-ring parameters, such as ring width (Deslauriers and Morin 2005). The growth, development and survival of a tree species requires an appropriate combination of space, light, water, temperature, mineral elements and atmospheric factors (Haferkamp, 1988; Kozlowski and Pallardy 1997). The number and proportion of particular cells produced during periods of cambial activity determine ring width and maximum density (Pritzkow *et al.* 2014).

Because of the expected negative effects of increased temperature and reduced water availability on the growth of tropical trees, the projected changes in global and regional climate pose a challenge for forest managers.

Due to climate change, water stress has increased, with drought affecting a substantially greater part of the world since mid-20th Century (Dai 2013). With a projected increase by up to 3.7°C in global mean surface temperature and in the frequency of dry spells by the end of the century (World Bank 2018), Miombo woodlands are projected to grow under increasingly harsh climatic conditions (Christensen *et al.* 2007; Makonda and Gillah 2007; Chirwa *et al.* 2014a; IPCC 2014a,b; Jew *et al.* 2016). For trees growing in drought-prone areas, growth rates and carbon fixation are expected to decrease in the long term, due to the predicted hotter and drier conditions (Pacheco *et al.* 2016). Stressors like drought not only constrain wood formation, but are also drivers of changes in anatomical features of wood (Pacheco *et al.* 2016; Warwick *et al.* 2017). In Zambia, the mean annual temperature (MAT) is projected to rise by 1.2-3.4°C by 2060, the number of hot days by 15-29% and the number of hot nights by 26-54% (World Bank 2018). During the same period, the mean annual precipitation (MAP) is expected to reduce from an average of 1032 mm to 800mm (McSweeney *et al.* 2008)

This chapter summarizes the findings of research into tree growth in the Miombo woodlands of Zambia and how it affects wood structure and quality. Using results from tree-ring studies and wood anatomical analysis, linear regression was used to predict quantitative changes in the ring width, as well as fibre and vessel characteristics (i.e. cell wall size, fibre width, diameter and number of vessels) for the studied species.

6.2 Modelling approach

The mathematical models for projecting future changes in wood anatomical properties were obtained using results of a study conducted to determine the growth response to climatic effects of three Miombo species (Munalula et al. under review). In this study, the known values of water availability (rainfall) over the years were correlated with wood anatomical properties.

Here, the known response of the selected wood characteristics (residual ring width, fibre and vessel characteristics) to previous changes in MAP are used to model the effect of projected MAP values obtained from various climate scenarios on wood anatomical properties. Across the sites and over Zambia in general, models indicate that precipitation will decrease (Figures 6.1 and 6.2).

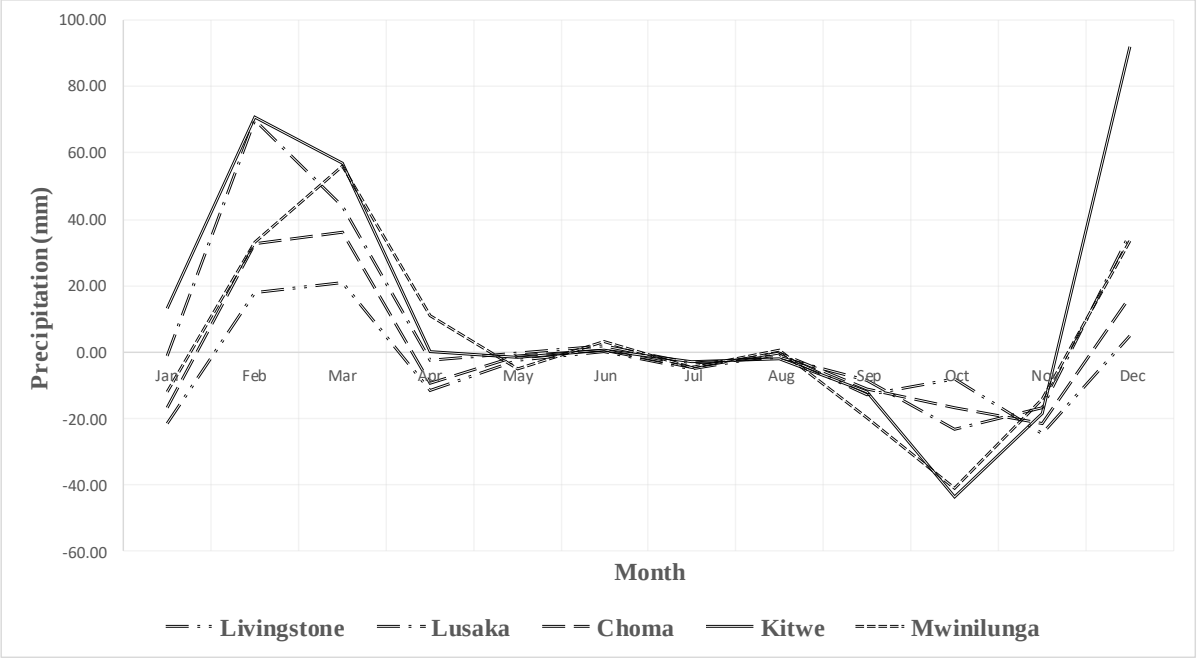

Figure 6.1: Projected change in precipitation for each site for 2020-2099

The projected changes in precipitation shown in Figure 6.1 for each site are based on emissions Scenario RCP8.5, model BCC_CSM1_1 while the future downscaled projected MAP for Zambia based on various models (World Bank 2018) is illustrated using Figure 6.2.

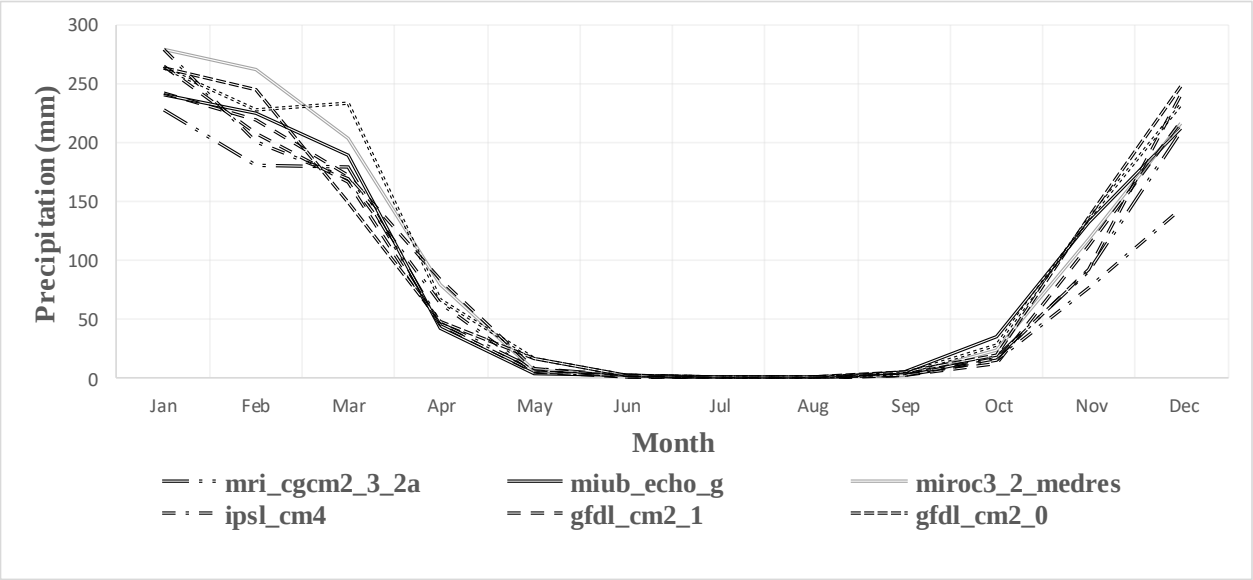

Figure 6.2: Projected MAP for Zambia for 2081-2100 by model.

Data from the BCC_CSM1.1 was used because most of the simulations used in predicting future climate are run by this climate system model (Wu et al. 2014; BCC, 2018). This model couples atmospheric, ocean, land, and sea-ice components, which "interact with each other through fluxes of momentum, energy, water and carbon at their interfaces" (BCC 2018b). The average values used in simulating future changes in climate range from hours to one year (BCC 2018).

For each anatomical variable, the anatomical values were plotted against projected rainfall data and least-square regression line was fitted to the data. The regression line was checked for linearity or the absence of non-linearity in the pattern of the data. The equation of the regression function for each property and species was determined, including the regression coefficient R, once a good fit model was determined.

6.3 Projected changes

6.3.1 Change in average ring width

Analysis of growth data indicates that among Miombo trees, decreased water availability during periods of cambial growth translates into decreased annual tree growth. Jaleel et al. (2009) and Shao et al. (2008) attribute reduced growth due to water stress to the negative effects of low turgor pressure on cell expansion and growth. The resulting regression functions had the form $Y = \alpha+\beta \cdot x$, where Y is the ring width, α and β are fit coefficients and x is the value of mean annual precipitation. The effect of change in MAP on residual ring width for each of the species is shown in Figures 6.3 and 6.4.

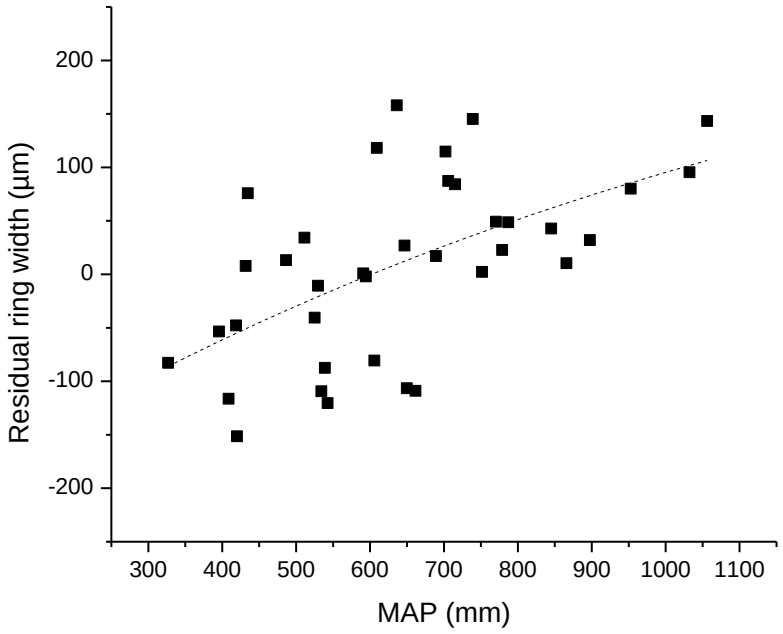

Figure 6.3: Relationship between residual ring width and precipitation in *Brachystegia spiciformis*

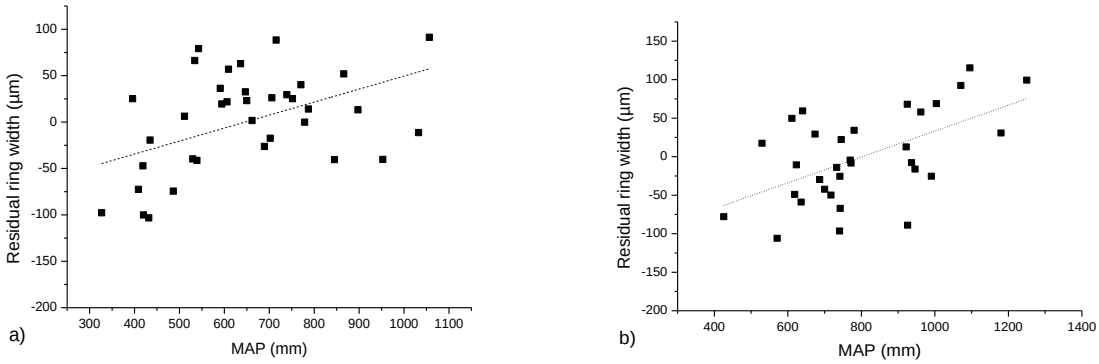

Figure 6.4: Relationship between residual ring width and precipitation a) *Burkea africana,* b) *Isoberlinia angolensis*

The linear regression model parameters for estimating the reduction in ring width (µm) per mm reduction in MAP for the studied species are presented in Table 6.1. For radial growth, the linear regression models are of the form $RW = \alpha + \beta \cdot x$. In the equation, *RW* represents the resulting growth ring width (for each species), α is the intercept, β is the slope of the line, and *x* is the MAP.

Table 6.1: Annual radial growth change with change in MAP.

Species	α	β	R	p-value
B. spiciformis	-162.08	0.264	0.57	<0.001
B. africana	-90.44	0.140	0.44	0.006
I. angolensis	-134.8	0.168	0.50	0.005

As can be seen in Table 6.1, the predictor variables for each of the species are significant, as their p-values are less than 0.05. Regression coefficients from the models indicate that for every 1 mm reduction in MAP the ring width can be expected to decrease by 161.8 µm in *Brachystegia spiciformis, 90.3* µm in *Burkea africana*, and 134.6 µm in *Isoberlinia angolensis*. Pearson's correlation test for all species (*Brachystegia spiciformis*; 0.57, *Burkea africana*; 0.44, *Isoberlinia angolensis*, 0.50) reveals a positive association of ring width with rainfall. Water stress and growth reduction will be higher in trees growing on the sites that already receive erratic rainfall and this will reflect in the ring structure. Response to water stress will also vary among the tree's organs and tissues. Poorter and Nagel (2000) found that during periods of water shortage, plants generally allocate more resources to root tissues compared to those allocated to shoots, resulting in a higher root:shoot ratio (Poorter and Nagel 2000).

6.3.2 Correlation of ring width and wood density

The growth rate / density relationship differs between ring-porous and diffuse-porous hardwoods (Adamopoulos *et al.* 2010; Malik and Abdelgadir 2015). In ring-porous hardwoods, wider rings are typically associated with higher wood density, because the early- and latewood proportions increase at the same rate (Panshin and De Zeeuw 1980; Zobel and van Buijtenen 1989). In diffuse-porous hardwoods, generally no relationship is found between growth rate and density (Malik and Abdelgadir 2015).

The influence of ring width on the wood density of the studied species was analysed through regression and, as expected for diffuse-porous hardwoods, little correlation of ring width with wood density was found. The linear regression model used to predict change in density with growth rate had the form $D = \alpha + \beta \cdot RW$ where *D* is the density, α and β are the coefficients for the equation, and RW is ring width.

The variation of density with ring width for the three species is shown in Figures 6.5 and 6.6.

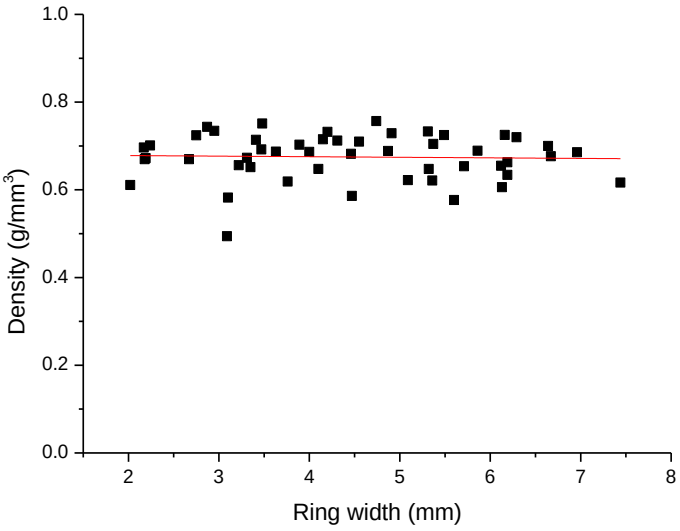

Figure 6.5: Density plotted against ring width in *Brachystegia spiciformis.*

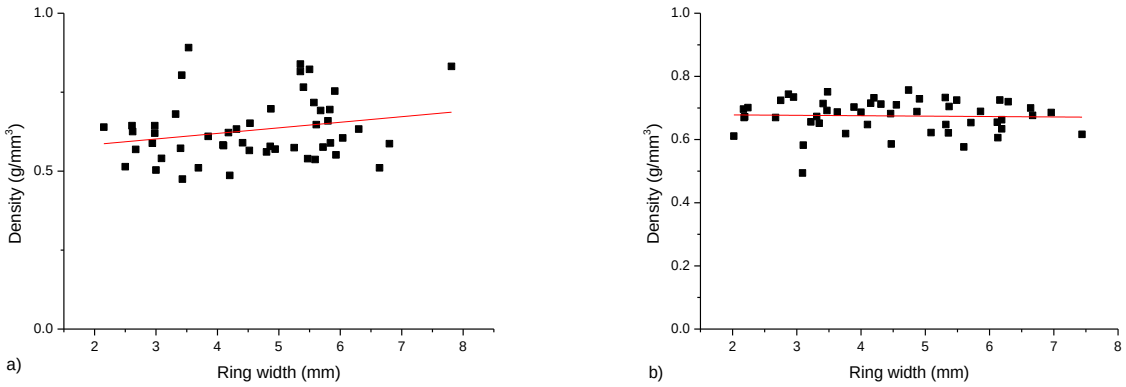

Figure 6.6: Density plotted against ring width in a) *Burkea africana*, b) *Isoberlinia angolensis.*

The fit functions and regression coefficients for each species are listed in Table 6.3. As can be seen from Table 6.2, the strongest relationship between ring width and density was in *Burkea africana* (R = 0.44) and the weakest in *Brachystegia spiciformis* (R = 0.33).

Table 6.2: Density change with change in ring width

Species	α	β	R	p-value
B. spiciformis	0.64	0.008	0.33	0.2
B. africana	0.55	0.018	0.44	0.4
I. angolensis	0.54	0.016	0.39	0.8

In diffuse-porous hardwoods, small and large vessels are evenly distributed across the growth ring. In all the species studied, the regression is not significant (p>0.05). The low correlation coefficient

(R) values for the three species indicate that very little of the density variation can be explained by the model.

6.3.3 Anatomical wood structure

Changes in environmental conditions result in changes in wood structure (Wimmer 2002). Because water availability during wood formation influences the characteristics of the xylem cells (Arend and Fromm 2007), significant differences can be expected in fibre and vessel characteristics with changes in mean annual precipitation.

The change in anatomical property (µm) per mm reduction in MAP for each species can be estimated using regression models of the form Y = a + b* exp(c*x), where Y is the value of the anatomical property of interest, a, b and c are coefficients, and *x* is the precipitation. For all the three species, this exponential model was used, because it showed the best fit to the available data.

6.3.3.1 Cell wall thickness

Figure 6.4 presents the relationship of cell wall thickness and MAP. The high R values indicates that a large proportion of the variation in cell wall thickness is caused by the variation in MAP. It is evident from Figure 6.7 that cell wall thickness decreases with increasing MAP. The effect is projected to be more significant on the drier sites, where wood with the thickest cell walls is found.

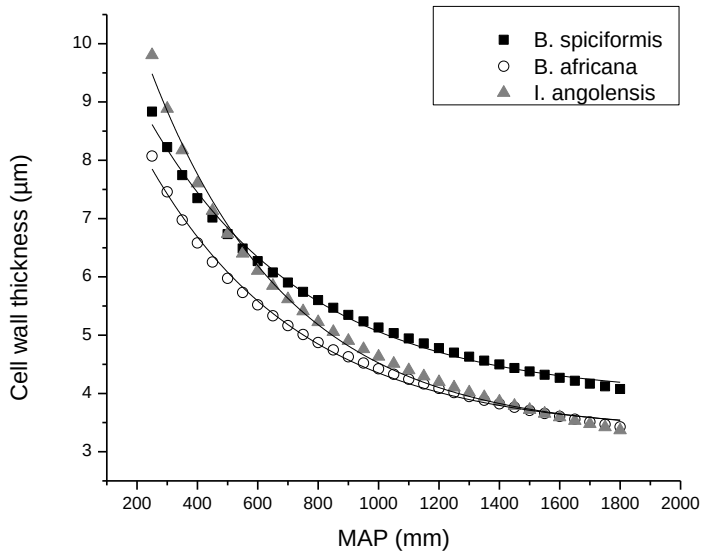

Figure 6.7: Cell wall thickness as function of precipitation.

Parameters of the exponential model explaining the projected change in CWT with change in MAP for each species are tabulated in Table 6.3.

Table 6.3: CWT change with change in MAP

Species	a	b	c	R
B. spiciformis	3.9	7.5	-0.0002	0.99
B. africana	3.3	7.4	-0.0002	0.99
I. angolensis	3.3	10.6	-0.0002	0.99

From the regression equations, change in MAP will have a greater impact on the CWT of *Isoberlinia angolensis* compared to that on *Burkea africana* and *Brachystegia spiciformis.* The regression functions indicate that *Burkea africana* and *Brachystegia spiciformis* will react the same. The regression coefficients indicate that for each expected 1 mm change in MAP, one can expect average cell wall thickness to change by 11.4 µm in *Brachystegia spiciformis*, 10.7 µm in *Burkea africana* and 13.9 µm in *Isoberlinia angolensis.*

Many recent studies (e.g. Roque and Fo 2007; Wiedenhoeft 2010) have shown that cell wall thickness directly affects wood density – with thicker cell walls resulting in higher wood density - and therefore the wood quality. The majority of mechanical wood properties depend on its cell wall thickness (Wiedenhoeft 2010).

6.3.3.2 Fibre diameter

Fibre diameter, as shown in Figure 6.8, will increase with increasing MAP. High R values (0.99) show that fibre diameter correlates positively with MAP for all three species. A reduction in MAP will therefore result in reduced fibre diameters, which translates into higher wood density.

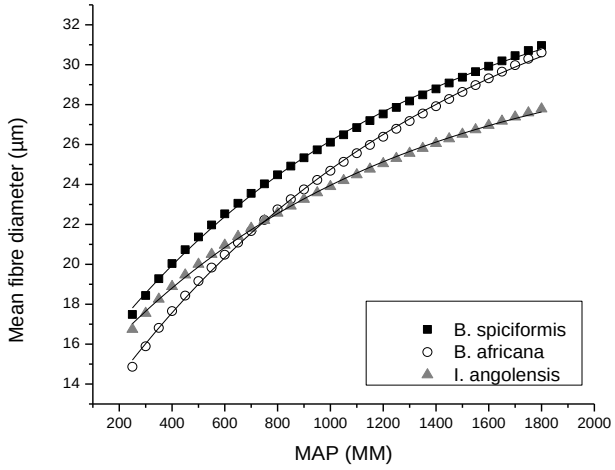

Figure 6.8: Fibre diameter as a function of precipitation.

The decrease in fibre diameter per mm reduction in MAP can be estimated using exponential regression models of the form *FD* = a + b * exp(c*x), where FD is the mean fibre diameter for the species. The regression models are presented in Table 6.4.

Table 6.4: Fibre diameter change with change in MAP

Species	a	b	c	R
B. spiciformis	35.4	-21.8	-0.0009	0.99
B. africana	37.2	-26.6	-0.0007	0.99
I. angolensis	31.1	-17.6	-0.0007	0.99

In all the three species there is a strong correlation between MAP and fibre diameter. In all three species, it can be expected that fibre diameter will decline with a reduction of MAP. For each 1 mm reduction in MAP, fibre diameter is projected to decrease by 10.6 µm in *Burkea africana*, followed by - 13.5 µm in *Isoberlinia angolensis* and 13.6 µm in *Brachystegia spiciformis.*

6.3.3.3 Vessel diameter

The relationship between vessel diameter and MAP, estimated using the equation of the form *VD* = a + b*exp(c*x), where VD is the mean vessel diameter for the species, is displayed in Figure 6.9.

The general trend shows that mean vessel diameter decreases with a decrease in water availability.

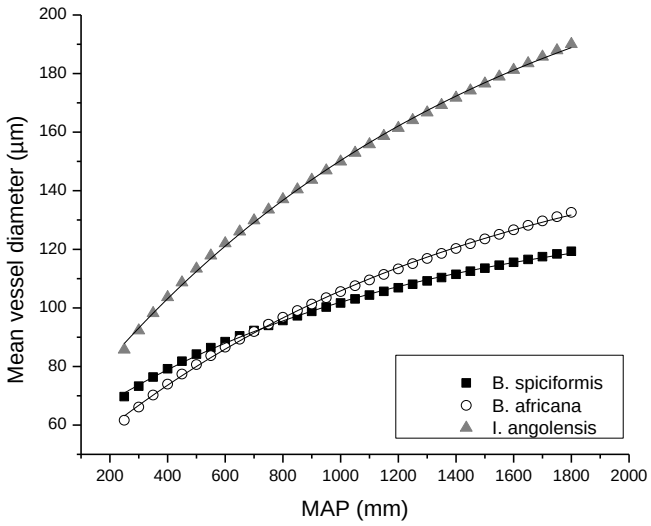

Figure 6.9: Vessel diameter plotted against precipitation.

Table 6.5 presents the parameters of the exponential models that explain the expected change in vessel diameter for each species with change in mean annual precipitation.

Table 6.5: Change in vessel diameter with change in MAP

Species	a	b	c	R
B. spiciformis	134.9	-79.8	-0.0009	0.99
B. africana	164.5	-121.7	-0.0007	0.99
I. angolensis	239.4	-180.9	-0.007	0.99

With high R values (0.99), all three species show a strong positive correlation between vessel diameter and MAP. An increase in MAP results in the production of larger vessels, which means that a greater area is occupied by voids thus translating into reduced wood density.

The projected reduction in MAP is generally expected to result in smaller vessels being formed. Regression coefficients from Table 6.5 indicate that the highest change in VD for every 1 mm change in MAP will be in *Isoberlinia angolensis* (-180.9 µm), followed by *Burkea africana* (-121.7 µm). The least change will be in *Brachystegia spiciformis* (-79.8 µm).

6.3.3.4 Vessel frequency

The vessel count was found to correlate negatively with MAP for all species and is illustrated in Figure 6.10.

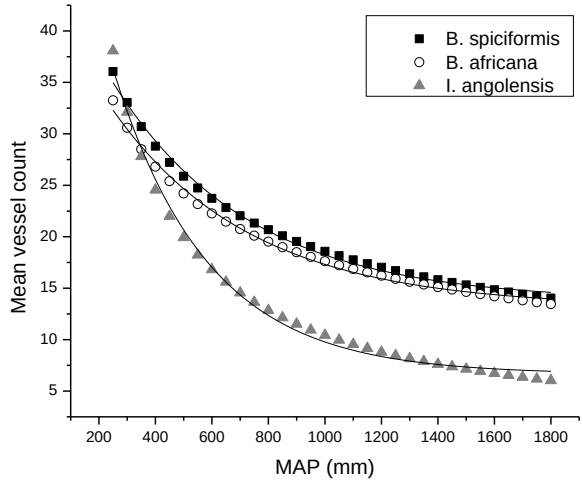

Figure 6.10: Variation of vessel count with change in precipitation

The parameters of regression models for projected change in vessel count with reduction in MAP for each of the species are presented in Table 6.6.

Table 6.6: Vessel count change with change in MAP.

Species	a	b	c	R
B. spiciformis	13.7	35.6	-0.0021	0.99
B. africana	13.1	31.8	-0.0023	0.99
I. angolensis	6.6	62.8	-0.0030	0.99

In all the three species, the number of vessels per unit of area correlates strongly (R = 0.99) with MAP. From the regression equations, the biggest change in mean VF with each 1 mm change in MAP is expected to be in *Isoberlinia angolensis* (66). Changes in mean VF in *Brachystegia spiciformis* (36) and *Burkea africana* (32) are projected to be almost similar.

In wood with less vessels per unit of area, the higher fibre-to-vessel ratio translates into higher wood density and therefore better wood quality.

6.4 Effect of change in growing conditions on wood quality

Dominant species from the genera *Brachystegia, Julbernardia,* and *Isoberlinia* are an important source of timber in Zambia and are used for applications, in which strength is a key consideration, with the main predictor for wood strength being wood density (Byers 2001).

The more heterogeneous the wood is, the more difficult it will be to use it for manufacturing various products.

Since wood density and fibre dimensions influence wood's structural, physical and chemical properties (Barnett and Bonham 2004; Roque and Fo 2007), density is often used as a measure of wood quality (Barnett and Jeronimidis 2009). Jozsa and Middleton (1994) cite higher strength, stiffness, and hardness as some of the properties that benefit from higher wood density. Therefore, any significant variation in density will make it difficult to predict the end-use characteristics of the wood (Lundqvist *et al.* 2017; Wessels *et al.* 2015).

6.5 Conclusions

Miombo trees are expected to grow under significantly changed conditions in future, consisting of elevated temperatures, reduced rainfall and frequent and severe droughts. Data analysis for all the species has shown that growth rates will decline, especially on the drier sites. Fibre and vessel characteristics will change with a change in water availability. Wood density, especially on the drier sites, can generally be expected to increase, but at the expense of volume growth.

If the mean annual precipitation for Zambia, as predicted using model bcc_csm1_1 under climate change Scenario RCP8.5, declines by 400 mm between 2080-2100, of the three species, *Isoberlinia angolensis* will have the largest increase in mean cell wall thickness (13.9 µm) and largest reduction in mean vessel diameter (69.2 µm). Due to increase in aridity, *Isoberlinia angolensis* will also have the largest increase in mean number of vessels per unit of area (60) compared to *Burkea africana,* which will have the lowest (43). Cell wall thickness, which will increase by an average of 10% (11.9 µm) across the species will have the biggest effect on wood density. Increased cell wall thickness will translate into higher density, which for most applications means higher wood quality.

Chapter 7 Conclusion and Recommendations

Tree growth and wood structure are affected by both long-term changes and irregular extremes of climate. Though it is not easy to quantify climate change in Africa, partly due to the diversity of sub-regional climates and the differences in geographic features (Tadross and Johnston 2012), noticeable changes in the long-term statistics of environmental factors have taken place across much of Southern Africa (Chidumayo *et al.* 2011; Kruger 2013; New *et al.* 2006). In Southern Africa the mean annual precipitation has declined, while records show that extreme weather events now occur more frequently, are more intense and last longer (New *et al.* 2006; New 2015). Additionally, trees growing in Southern Africa have to cope with significant (-23% to +33%) inter-annual rainfall variability (New 2015).

General circulation and other models indicate that trees in Southern Africa will grow under harsher conditions in the years ahead. MAT will rise by up to 4°C in the next 50-100 years (Lesolle 2012; IPCC 2013). Below normal rainfall is expected in the region, characterised by periods of droughts in some areas and floods in others (IPCC 2014b). For this reason, managers and users of forest resources must plan for and deal with the challenges posed by and the impacts climate change has.

Not much research has been published on how the hardwood trees growing in Southern Africa have adapted to changing climatic conditions despite evidence from several studies showing that growing conditions have changed.

The first phase of this study looked at global, African and Southern African climate trends, the stress concept and how trees respond to both short- and long-term stress, the concept of limiting factors, the key climatic factors affecting tree physiology, growth and wood structure, and how dendrochronology could be used to gain insights into the relationship between climate and tree growth. The focus of this study was on stress resulting from changes in factors that directly affect growth (water and temperature). A stressful environment affects tree growth by altering physiological, biochemical and molecular processes (Ashraf and Harris 2013). Of all the factors necessary for growth, the scarcest essential factor is what limits growth (Kozlowski 1971; Fritts 1976; Kozlowski and Pallardy 1997; Nabeshima *et al.* 2010).

Despite the evident changes in growing conditions, little is known about how Miombo trees respond to changing climatic conditions. Since most indigenous forest systems are not able to use eco-physiological process models and there is a general lack of long-term growth data, it was decided that a retrospective growth ring analysis approach would be appropriate (Downes *et al.* 2009; Jacoby and D'Arrigo 1997).

To better understand the effect of climatic factors on Miombo species, differences in annual growth and anatomical wood properties were analyzed and quantified for trees from different sites. By obtaining the properties for sites ranging from dry to wet, as well as looking at the annual variation in temperature and water availability, the results were used to predict future changes in tree growth and wood structure with the expected reduction in mean annual precipitation. Firstly, the sites were characterized based on aridity indices, which take the mean annual precipitation into account, as well as the mean annual temperature.

To compare annual growth across the sites, samples, in the form of increment cores, were obtained from between 15-20 trees per species from each site where they were available. Standard dendrochronological procedures (Grissino-Mayer 1999; Speer 2010) were used to prepare the samples for ring measurement. The sample trees varied in tree age, diameter at breast height (DBH) and in total height. Analysis of variance for each of the species revealed that differences in growth response between sites were considered statistically significant ($p<0.05$). For all species, trees growing on the driest sites showed more sensitivity to changes in aridity. In *Brachystegia spiciformis,* mean sensitivity ranged from 0.36 on the wettest site to 0.59 on the driest site. *Burkea africana* also showed a similar trend with a low means sensitivity (0.32) at the wettest site and a high mean sensitivity (0.44) on the driest site. In *Isoberlinia angolensis* the wettest site had a mean sensitivity of 0.33, while the driest had a mean sensitivity of 0.46. Mean sensitivity had a strong negative correlation with precipitation and all species showed complacency on wet sites. There was a moderate but positive correlation of ring width with precipitation. Though several confounding factors act on a tree as it grows, about 20% of the variance in ring width could be explained by precipitation. The effect of temperature was found to be insignificant.

To understand how wood structure is affected by the climate, the residual ring width was plotted together with aridity index as a function of time. From the graph, a very dry year and a very wet year were selected, and these sections were cut out from two cores from 5 trees per species per site for wood anatomical studies.

In all the species, statistically significant differences ($p<0.05$) were observed in the fibre and vessel characteristics of wood formed during the wet and dry year and in the wood from sites differing in water availability. The thickest cell walls were found in wood formed during dry years in in wood from drier sites. In all the species, mean cell wall thickness in the dry year negatively correlated well with DMI ($R = -0.98$ for *B.* spiciformis, $R = -0.97$ for *Burkea africana* and $R = -0.98$ for *Isoberlinia angolensis*). High correlation factors ($R=0.92$ for *Brachystegia spiciformis*, $R=0.98$ for *Burkea africana* and $R=0.98$ for *Isoberlinia angolensis*) were also found in the wet year. Numerous studies (e.g. Eilmann *et al.* 2011; Eilmann and Rigling 2012; Kreuzwieser and Gessler 2010; Lundqvist *et*

al. 2017; Wagner *et al.* 2012) have established a strong link between limited water resources and slower growth and thicker cell walls.

Significant differences ($p<0.05$) were also noted for the fibre diameter between-sites and between wet and dry years. On the wet sites, no evidence of significant differences ($P>0.05$) in the FD means between wet and dry years was found. In all species, the narrowest fibres were found in wood from dry years and in wood from the drier sites. For all species mean FD correlated positively with DMI both in the dry year (R=0.87 for *Brachystegia spiciformis*, R=0.97 for *Burkea africana,* and R=0.98 for *Isoberlinia angolensis*) and in the wet year (*Brachystegia spiciformis* R=0.95*; Burkea africana,* R=0.99; and *Isoberlinia angolensis,* R=0.98).

The vessel frequency differed significantly between dry and wet sites ($p<0.05$) and more vessels were found per unit area in wood formed on dry sites. Drew *et al.* (2009), Fonti *et al.* (2013) and Naidoo *et al.* (2007) also reported a larger number of vessels with reduced vessel size in hardwoods growing in a water-limited environment.

The correlation between ring width and wood density was determined for all species across the sites and the results indicated that the influence of ring width on density was insignificant. This was not surprising considering the diffuse-porous nature of the sample species.

Using the established values of ring, fibre and vessel characteristics, fit functions were developed to predict the response to future climate changes. Modelling was based on projected values of rainfall and temperature in the next three to five decades, to obtain a likely change of wood properties with a changing climate in the future. The models revealed that cell wall thickness, which will increase by an average of 10% (+0.6 µm) across the species, will have the biggest effect on wood density. Of the studied species, *Isoberlinia angolensis* is projected to have the largest increase in cell wall thickness (+0.83 µm) and largest reduction in vessel diameter (-20.2 µm).

Because many wood properties are related to its structure and density (Roque and Fo 2007), density is often used as a measure for wood quality (Barnett and Jeronimidis 2009). Higher wood density typically translates into higher strength, stiffness and hardness (Jozsa and Middleton 1994). Large variations in wood properties are undesirable since they affect the end products made from it.

While earlier studies by (Trouet *et al.* 2001; Fichtler *et al.* 2004; Trouet 2004; Syampungani *et al.* 2010; Ngoma *et al.* 2017) were aimed at proving that Miombo species had visible growth rings and could be used for dendrochronological studies, this study could show that climate variability can be studied using the wood structure of these trees. Furthermore, it was successfully attempted to predict how a future changing climate will affect wood density and, with it, wood quality of three species of economic value.

Based on measurements made and results obtained, *Isoberlinia angolensis* will change its properties most due to climate change, becoming denser on the drier sites while not changing much on the wetter sites. *Burkea africana* will change least compared to the other two. The changes that will occur will affect all mechanical and physical properties of wood. This means wood quality, depending on desired applications will change.

Further studies should be carried out involving other Miombo species, especially those of commercial value, to determine how they react to variations in rainfall. Additionally, it is recommended that differential growth of Miombo species growing under similar climatic conditions should be studied.

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